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NOTES ON THE ECOLOGY OF THE DARK RICE FIELD MOSQUITO, PSOROPHORA CONFINNIS, IN COACHELLA VALLEY, CALIFORNIA (DIPTERA: CULICIDAE)[1]

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ABSTRACT

P. confinnis occur in a variety of temporary waters in this area in southern California, but on many ranches larvae were found only in irrigated date lanes. Here larval-pupal densities are higher in grassy areas and under pruned date fronds than in areas bare of cover, and larvae concentrate near cow droppings. Size of fourth-instar larvae tends to vary inversely with larval density. Fourth-instar larvae and pupae were once observed completing their development in muddy areas where irrigation water had disappeared from the surface. In the laboratory they can do so on moist filter paper, but third-instar larvae develop no farther. Larvae and pupae are attracted to light at night. Water persists in the date lanes for an average of 5.1 days after each semi-monthly flooding; the aquatic development of *confinnis* can be completed within this time only at water temperatures of 26° C. or higher. Hence adults are numerous only from mid-June through September. The scarcity or absence of adults on irrigated ranches lacking livestock suggests that cattle are the necessary principal host. Females usually cannot pierce human skin until 4 hours after emergence; to survive they must feed within 24 hours. Adults are nocturnal and both sexes are attracted to lights. Trap-light captures reach a peak 2 or 3 hours after sunset. During the day adults cling to grasses, especially over moist or soggy soil, and fly only a few meters when disturbed, usually at a height of 1 meter or less. Males disappear rather abruptly but the female population declines slowly as the soil dries. Tests show moist soil with grass cover strongly preferred for oviposition, and moist soil without cover, water, and dry soil are progressively less attractive. Toxaphene, ¾ gallon in 50 gallons of water per 5 acres, kills second- and third-stage larvae, but is ineffective against older aquatic stages. Control possibly could be achieved by changing the irrigation regime so that water would persist in the lanes only 3 or 4 days after each flooding.

Psorophora confinnis (Lynch Arribalzaga) is an important pest in certain regions having considerable areas of temporary water. It may form 80 percent or more of the total mosquito population (Schwardt 1939). In the rice growing areas of Arkansas, where *confinnis* possibly reaches its greatest abundance, and in the Florida Everglades, reduced milk production and occasional deaths of livestock are attributed to bites of this mosquito (Bishop 1933). Cattle are the chief source of blood, while horses, mules and hogs are fed upon less frequently (Whitehead 1951). Humans are fed upon infrequently, probably because they are usually protected by screening at night when *confinnis* is active. However, this species attacks and bites severely when disturbed during the day.

P. confinnis was first reported in California in 1940 (Aitken 1940), and since then has become the most important summer pest in the Coachella Valley in Riverside County. It is particularly troublesome to workers tending date trees and other irrigated crops centered around Indio. The 4,800 acres of date groves in the valley provide an excellent breeding habitat for *confinnis*.

The field work of the present study was carried out by the senior author in the summers of 1954 and 1955, in cooperation with the Coachella Valley Mosquito Abatement District (CVMAD). This is the initial work on the biology of *P. confinnis* in California. It provides an interesting comparison with the ecological work on this species in Arkansas (Horsfall 1942, Schwardt 1939). In comparison with Arkansas, the Coachella Valley is a hot desert valley. The average yearly rainfall is 3.34 inches; half of this falls in December, January and February. The months of April through July are usually rainless. Mean monthly temperatures range from 53.8° F. in January to 93.1° in July; the yearly mean temperature is 73.3° F.

[1]The present paper summarizes the thesis presented by the senior author in partial fulfillment of the requirements for the M.S. degree in the Department of Biology, University of Southern California. The thesis work was planned and carried out under the guidance of the junior author. Accepted for publication December 8, 1958.

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Most of the field work was done on four adjacent date ranches, totalling about 500 acres, in the village of Thermal, California. On these ranches date trees are planted in rows on irrigation dikes, the dikes alternating with irrigation lanes about 50 meters by 7 meters. These lanes are usually flooded twice a month, and standing water remains 3 to 8 days each time. Records for 17 periods of irrigation on 109 lanes showed an average persistence of water for 5.1 days. Usually groups of lanes are irrigated in rotation, so that at any one time there are present some lanes covered with water, some having moist soil, and others with dry soil. Livestock were kept on three of the four ranches in the study area.

tion in the area. In addition, data of the CVMAD were available for seven other traps located in the valley outside the study area; these traps were routinely emptied every 3 or 4 days.

Density of adult mosquitoes in specific areas was measured by standard sets of 48 sweeps with an insect net of 30 cm. diameter. It is assumed that 48 sweeps capture a sample of mosquitoes equal to that occurring over 1 square meter of surface in the sampled area (Whittaker 1952).

Density data were compared with climatic data. A distance-bulb recording thermograph was used to make continuous records of water temperatures in flooded date lanes. In addition, water temperatures of other irrigation lanes were measured

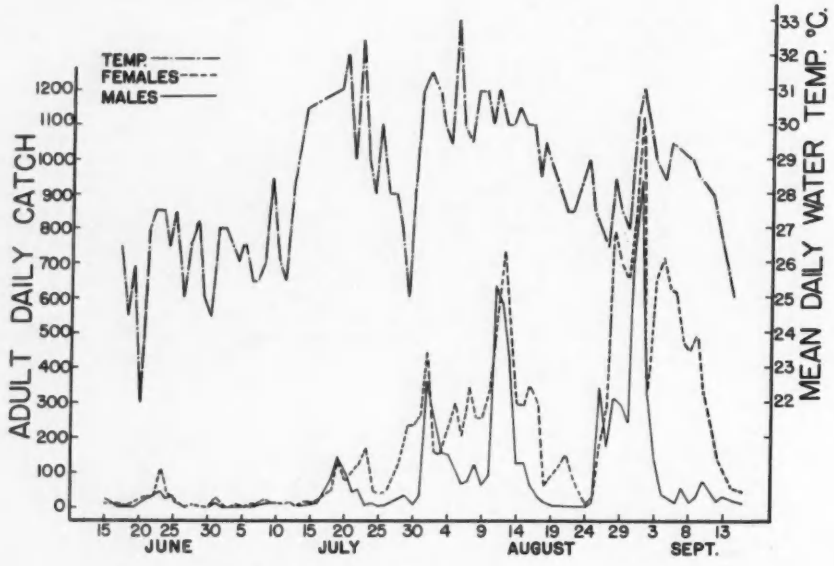

FIG. 1.—The mean daily water temperature and the nightly catch of *Psorophora confinnis* in one New Jersey light trap located in the study area, June 15 to September 15, 1955.

The authors gratefully acknowledge the assistance of Dr. E. R. Tinkham, manager and entomologist of the CVMAD in 1954, who suggested the problem. Thanks are also due to Mr. Cavenoph, manager in 1955; to the trustees of the Coachella Valley Mosquito Abatement District for use of data, equipment, and laboratory space of the District; and to the employes of CVMAD for their help and cooperation.

METHODS AND MATERIALS

Density of adult mosquitoes.—A New Jersey light trap was operated continuously in the study area from mid-June to mid-September 1955. The nightly catch of this trap was used as an index of changes in the size of the adult popula-

daily at 7 a. m. and 4 p. m. with a mercury thermometer. Air temperatures were obtained from records of the weather station of the U. S. Date Gardens, Indio, California, about 7 miles from the study area.

Egg-laying habits.—Engorged females were placed in a wire mesh cage, 46 x 34 x 47 cm., kept in the field, and their reaction to several experimental surfaces simulating the surfaces of irrigation lanes was measured. The surfaces, prepared in 10 cm. petri dishes, were: water, moist soil, dry soil, moist soil with grass stems stuck into the soil. The number of eggs laid in each dish was counted after 4 or 5 days, exposure.

Larval-pupal densities.—Densities of the aquatic stages were measured as the average number of

individuals caught per dip in six standard dips with a dipper 11.5 cm. wide and 7 cm. deep. The dipper was moved quickly about 40 cm. each dip.

RESULTS AND DISCUSSION

Seasonal occurrence of adults.—Light-trap records of the CVMAD for 1952–1955 show that good populations of *P. confinnis* have occurred from mid-June through September. As shown in figure 2, population buildup and decline are abrupt. Maximum population occurred at different times in these 4 years, ranging from the third week of August to the fourth week of September. Adults were captured as early as April 16 and as late as October 29.

A comparison of weekly air temperatures and weekly light-trap catches of CVMAD for 1955 (fig. 2) shows that no adult *confinnis* were caught between January 1 and April 21, when mean weekly air temperature averaged 14.9° C. Adults were continuously present from April 28 through October 20, when weekly air temperatures averaged 28.2° C. From June 21 through October 6, when the largest catches occurred, mean weekly air temperatures averaged 30.5° C.

The occurrence of 26° C. as the threshold of population development depends on the interaction between the rate of aquatic development of *confinnis* and the length of persistence of irrigation water. Horsfall (1942) showed that *P. confinnis* requires 7.0±0.1 days to complete its aquatic development at 26° C. in the laboratory, and 5 to 6 days at water temperatures ranging from 30° to 35° C. in the field. In the present study area, which is typical of the Coachella Valley, irrigation water persists an average of 5.1 days, and occasionally stands for 7 to 8 days. From June 15 to July 11, 1955, when water temperature averaged 26.2° C., the emerging of some few adults was possible, in lanes that remained flooded 7 to 8 days. Large populations were possible only when the water temperature had in-

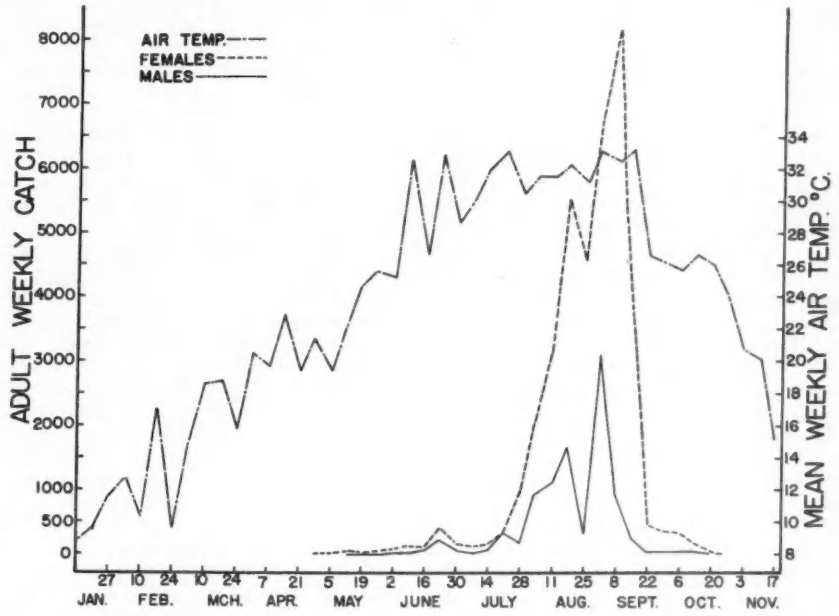

FIG. 2.—The mean weekly air temperature and weekly catches of *Psorophora confinnis* in eight light traps located in Coachella Valley, California, in 1955.

creased to the point where development could be completed or nearly completed within 5 days. As will be discussed later, some development can be completed on moist soil, after disappearance of surface water.

Adult density and habitat conditions.—The highest densities of adult *confinnis* were found over soggy soil. Average densities over soggy, moist, and dry irrigation lanes were 56.5, 20.1 and 4.2 individuals per square meter respectively. As the soil of a lane dried out, the population of female *confinnis* declined smoothly, while the male density declined abruptly as the soil changed from a soggy to a firm but still moist condition. Male density over dry soil was 0 to 1 per square meter.

Females collected over soggy soil were largely unfed, newly hatched individuals, while those from over moist or dry soil were mostly engorged.

The presence of a grass cover makes an area more attractive to adult *confinnis*. Ten sets of sweeps each over grass covered and bare areas of moist soil gave average densities of 32.1 and 8.2 per square meter, respectively.

Adult density and presence of livestock.—During August and the first half of September 1955, densities of adults were measured at 40 different ranches, 20 keeping livestock and 20 without. Four sets of sweeps through grasses growing on moist soil were taken at each ranch. The ranches having livestock had an average density of 9.8 *confinnis* per square meter. Three of these ranches had no mosquitoes, two for no apparent reason, and one because of sandy soil that did not retain water long enough for aquatic development of *confinnis*. Of the ranches without livestock, one had a density of 12.3 *confinnis* per square meter, while the other 19 ranches had an average density of 0.16 per square meter. No *confinnis* were taken on 12 of these ranches.

This obviously demonstrates a feeding relationship. Whitehead (1951) has shown that cattle are the preferred blood source of *P. confinnis*. An immediate blood meal, plus at least one feeding later, is needed for survival of females until the time of egg laying (Horsfall 1942).

Adult daytime behavior.—During the day adult *confinnis* cling to the stems and leaves of grasses, about 20 cm. above the ground. They don't leave their resting places unless disturbed by movement of an animal or person in their vicinity. Air movements and shadows do not disturb *confinnis*. When disturbed, *confinnis* usually fly no higher than 100 cm. and return to grass cover after covering a linear distance of 300 cm. or less. Sweeps made while moving through grass, with the net at a height of 120 cm., rarely capture *confinnis*.

Adult nighttime activity.—*P. confinnis* is very active after dark, and becomes so irritating that most people find it difficult to stay out-of-doors. The senior author found it particularly difficult to be in the date groves at night.

Quantitative changes in night activity were measured by making frequent collections at a light trap in the study area. There is little activity just before sunset; activity reaches a maximum 2 to 3 hours after sunset, and then gradually decreases. Following is the average catch per hour per day for the period August 29 to September 12, 1955 (average time of sunset 6:20 p. m.): 5–6 p. m., 0.4 individuals per hour; 6–7 p.m., 94; 7–8 p. m., 193; 8–9 p. m., 125; 9–10 p. m., 83; 10–11 p. m., 57; 11–12 p. m., 41; 12–1 a. m., 33; 1–5 a. m., 14.

Feeding habits.—Newly hatched females show biting behavior similar to older females when they are placed on a human arm, but they cannot pierce the skin. Of six females tested, one bit and became engorged within 4 hours after emergence; two others were able to fully engorge in 15 hours; one pierced at six points but did not fully engorge and two did not bite within 15 hours.

A female may probe many locations before inserting its proboscis. The proboscis is inserted at different angles, from very acute to perpendicular. The female sucks blood for about 5 minutes at each feeding and discharges small drops of a watery fluid from the tip of her abdomen at 5-second intervals during this time. A fully engorged female is unable to fly and cannot cling to a surface if it is agitated slightly.

Unfed newly emerged males all died within 24 hours when confined in quart containers in the laboratory or field. Most females also died within 24 hours, but a few survived up to 120 hours. The short life span of the males undoubtedly accounts for their rapid disappearance after irrigation water is gone.

Egg-laying habits.—Engorged females given a choice of different experimental surfaces in a cage showed a very definite preference for moist soil with "grass cover." In three experiments providing a choice among petri dishes with moist soil, dry soil, and water, an average of 294 eggs were laid on the moist soil, 53 in the dish with water, and 0.3 on the dry soil. In one experiment offering moist bare soil versus moist soil with grass stems stuck in it, 8 eggs were laid on the bare soil and 117 on the soil with "grass cover." Field observations support this experimental observation. In two adjacent lanes, one grassy and one bare of vegetation, the larval densities were 20 per dip and 1 per dip, respectively.

Carpenter and Lacasse (1955) and Horsfall (1942) have previously observed *confinnis*' preference for moist soil, while Matheson (1944) claims that *confinnis* lays its eggs on dry ground. Horsfall (1942) found that areas planted with rice provided good egg-laying sites, while areas bare of vegetation were of little importance.

In the above experiments, eggs were found laid singly and in groups of 2 to 20; the eggs in a group were not glued together. Most of the eggs were found in small holes or clefts in the soil, or behind small bits of plant material. Some

eggs were laid between the edge of the soil and the glass wall of the dish.

The egg-laying habits of *confinnis* determine that only one generation can develop as the result of each irrigation. Flooding causes the hatching of the eggs that are present in the dry soil of a lane, these eggs having been laid in the soil while it was still moist from the previous irrigation. As the irrigation water recedes, new eggs can be laid in the moist soil, but these eggs cannot hatch until the next flooding. Horsfall (1942) observed in Arkansas that the peaks of abundance of *P. confinnis* followed the pattern of irrigation of the rice fields.

Since an entire lane is flooded in a relatively short time, the eggs in it hatch almost simultaneously and the individual mosquitoes develop in step. It was repeatedly observed that one developmental stage was completely dominant at one particular time. Near the end of aquatic development, many pupae, some fourth-instar larvae, and very few individuals of earlier instars were present.

The density of individuals in a particular lane increases as the area of open water recedes, and then abruptly decreases as the pupae transform. Pupal densities of more than 200 per dip were observed in very small pools of rapidly drying lanes.

Types of larval habitats.—Larvae of *P. confinnis* were found in a great variety of situations in addition to date irrigation lanes: small puddles from dripping faucets and evaporative coolers, small patches formed by leaking irrigation pipes, irrigation standpipes, roadside ditches, flooded pastures and flooded areas of a local duck club. However, date irrigation lanes were the only place *confinnis* were found on many of the ranches visited. Special attention was given to standpipes. Of 189 standpipes whose tops were above ground surface, 46 contained water, but none had larvae. Of 41 pipes whose tops were slightly below ground surface, 21 contained water, 8 with larvae. Larval density averaged 4.4 per dip in these 8 pipes. Apparently standpipes are not important breeding sites for *confinnis*.

Densities in microhabitats.—Larval and pupal densities varied within a particular water area according to microhabitat conditions. Higher densities were found in areas with a cover of vegetation than in bare areas. Measurements in 8 lanes showed an average density of 18.3 larvae and pupae per dip in grassy areas, compared to 1.2 per dip in adjacent areas without vegetation. In 2 lanes, larval densities were 7.5 per dip in water covered with pruned palm fronds and only 0.4 per dip in nearby open water.

Higher densities are found in the immediate vicinity of cow droppings. In one pool, a density of 39.5 larvae per dip was found near cow droppings, compared to 5.1 per dip 1 meter away. Two adjacent patches of water of about 1 square meter, connected to a large water area, showed 119 larvae per dip in one patch containing droppings and 74 per dip in the other patch without droppings. This indicates that there is a possible attraction of larvae to manured areas, possibly because microorganisms concentrated there provide food for the larvae. The occurrence of livestock in the breeding area of *P. confinnis* is not only necessary for the feeding of the adult females, but it is also beneficial to the larvae.

Water pH in various microhabitats varied from 5.5 to 8.0, but usually was between 6.4 to 7.0. No relationship was found between larval-pupal densities and pH.

Larval size and larval density.—It was noticed in the field that fourth-instar larvae were not all the same size. "Giant" larvae were generally found in areas where density was low. At densities of 5 to 17 per dip the length of larvae averaged 8.8 mm., while at densities of 45 to 86 per dip the length averaged 7.2 mm. This probably demonstrates the effect of competition.

Larval behavior.—Various aspects of behavior were observed in the laboratory and field. Larvae typically move back and forth between the surface of the water and the bottom, spending a short time at each place. Measurements on 120 third- and fourth-instar larvae showed an average of 29.4 seconds spent on the bottom each time and 16.6 seconds at the surface, i.e., about twice as much time spent on the bottom as at the surface. However, 60 other fourth-instar larvae averaged 24.4 seconds per stay at the bottom versus 50.1 seconds at the surface. These larvae were probably nearing the time of pupation and this may account for the difference in time at surface. Moderate changes in water temperature and depth did not seem to influence this behavior.

When at the surface, larvae rest quietly at an angle of 45°, or graze with the body parallel to the surface, moving either forward or backward. Sometimes an S-shaped position is assumed, often followed by defecation. Larvae graze at the bottom with the head in the mud and the body at a 45° angle; while grazing, the larvae move along smoothly, without wriggling, except when moving to a new location. Ascending to the surface is accomplished by continuous or interrupted wrigglings. Diving takes place slowly, at an angle of 30°, with or without wriggling.

Normal activity ceases when larvae are exposed to 9° or 40°–41° C. Larvae kept 12½ hours at 9° C. were all immobile, either at the bottom or surface. Normal movements were recovered in 3 hours, after the water had warmed to 27.5° C. Only 5 percent of larvae tested survived 15 days of 9° C. Larvae remained inactive at the surface after 10 minutes at 40–41° C. However, pupae in the same water remained active and normal. This greater temperature tolerance of pupae is of considerable value in that pupal development

usually occurs in very shallow water, or on the surface of soggy soil, while the larvae are usually protected by the buffering action of deeper water.

Five studies were made at night using a flashlight to illuminate a circle of water 30 cm. in diameter. Larvae and pupae swam toward the light and concentrated immediately below it. Larval-pupal densities under the light averaged 38.5 per dip versus 2.7 per dip 1 meter from the light.

Pupation and emergence of adults.—Previous to shedding its skin, the larva hangs down from the surface without moving. Stretching movements then occur and are followed by strong peristaltic movements, from the posterior end forward. The larval skin splits in midthorax, the pupal respiratory trumpets protrude and are raised to the surface as the larva swings parallel to the surface, and then about 30 peristaltic waves gradually push the skin to the tip of the abdomen where it usually immediately falls off. The pupa then bends its abdomen forward and downward, assuming the typical comma shape. The time for ecdysis, from appearance of respiratory trumpets to complete shedding of the skin, is about 1 minute.

When the adult is ready to emerge, the pupa hangs just below the surface with trumpets open to the surface. The mesonotum of the adult appears through a slit between the trumpets. The head and proboscis, and then the rest of the body emerge in a series of strong outward pushes, followed by weak withdrawals. The newly emerged adult clings to some surface until it is strong enough to fly.

Resistance to desiccation and development out of water.—A fortunate observation led to the development of this topic. CVMAD workers left several small patches of water unsprayed in a particular control operation, reasoning that the water would dry up before the aquatic development of *confinnis* could be completed. The senior author visited this area 24 hours after the disappearance of surface water and found fourth-instar larvae and pupae alive in the mud. Several newly emerged adults were captured, and active larvae and pupae were recovered by placing mud scrapings in water.

Different instar larvae and pupae were then tested for their ability to survive and develop on moist filter paper in covered petri dishes kept at room temperatures of 24° to 31° C.

The success of development depends on the stage at which surface water disappears (or is experimentally removed). Third-instar larvae were not able to develop further in petri dishes, probably because they could not feed. Of 28 larvae in one dish, 50 percent survived 42 hours, but all were dead after 66 hours. Fourth-instar larvae usually pupated in the dishes. Of 160 such larvae in 10 dishes, 150 pupated, and from these pupae 70 adults emerged. Thus 43.7 percent of fourth-instar larvae were able to complete their development. Pupation in the dishes was completed within 10 to 20 hours and emergence of adults occurred between 32 and 45 hours after the larvae were placed in the petri dishes.

Pupae were very successful in developing in the dishes. This is to be expected, since even in water the pupae do not feed, but utilize stored energy for their transformation. From 402 pupae collected in damp mud and placed with the mud in a dish, 365 adults emerged, a survival of 90.8 percent. This is twice the recovery of adults from fourth-instar larvae.

This completion of development on a moist surface may be of considerable importance to *P. confinnis* in nature. Surface water frequently disappears before adult *confinnis* are able to emerge. The experiments with fourth-instar larvae suggest that 3 to 4 days of development in water at 30° to 35° C., plus 2 days in mud, may be sufficient for completion of metamorphosis.

Effectiveness of Toxaphene against P. confinnis.—The senior suthor made several observations on irrigated areas before and after the application of the larvicide, toxaphene, by CVMAD workers. Toxaphene was applied for control of all species of mosquitoes at a rate of ¾-gallon toxaphene in 50 gallons of water per 5 acres. Application was by spraying from a jeep-borne sprayer. The author's observations agreed with the experience of CVMAD workers, that toxaphene thus applied is highly effective against first- to third-instar *confinnis*, partially toxic to fourth-instar larvae, and ineffective against pupae. In three experiments various instars were collected from sprayed lanes, kept in water from these lanes, and observed for survival. All second- and third-instar larvae died about 22 hours after application of the spray. Of 30 fourth-instar larvae in one collection, 22 survived to pupate, and 17 adults emerged 50 hours after spraying. In a second group of 78 fourth-instar larvae, 26 pupated and 21 adults emerged. Twenty adults emerged from 23 pupae taken from sprayed water.

In a field study, two lanes, which had second- and third-instar densities, respectively, of 26 and 59 per dip immediately before spraying, dropped to 0 and 0.7 larvae per dip 24 hours after spraying.

In another study, two lanes were sprayed 12 hours before they were flooded (prelarviciding technique), and then compared with an adjacent untreated lane. The second day after irrigation the prelarvicided lanes had densities of 7.4 and 74.5 larvae per dip, while the control lane had 10.3 per dip. The effect of prelarviciding is dubious in this case.

The results of this study of *Psorophora confinnis* strongly suggest that biological control of this mosquito could be attained by changing the irrigation regime so that irrigation water would not stand in the lanes longer than 3 to 4 days.

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NOTES ON THE LIFE HISTORY AND HABITS OF CERAMIDIA BUTLERI MOESCHLER, A PEST OF BANANAS (LEPIDOPTERA: SYNTOMIDAE)[1]

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ABSTRACT

Eggs hatch in 5 to 6 days, larval life with its 6 to 7 instars requires 18 to 23 days, and the pupal stage averages 9 days. Eggs are laid and larval life is passed on the under side of banana leaves; pupation usually takes place there also, but sometimes occurs behind the leaf sheaths on the side of the pseudostem. During its last instar, which has the longest duration, the larva consumes more leaf tissue than during all preceding instars together. The medium-sized, bluish-black adults are very active during the days. Laboratory-reared adults lived from 3 to 6 days. This species is a serious pest of bananas in Costa Rica, where these observations were made.

A number of lepidopterous larvae are important pests of banana plants in tropical America. Species of the genus *Ceramidia* constitute some of the most important. Cockle (1904, 1910) and Cockerell (1910) reported adults of *Ceramidia butleri* collected from imported bananas in North America. Cevallos (1957) reported *Ceramidia viridis* Godman to be a serious pest of bananas in Panama. In Costa Rica the most destructive of these is the caterpillar of *C. butleri* which damages the plant by feeding on the leaves, thus reducing the leaf surface and shortening the life of the leaf. During times of high caterpillar population, damage to the plants is so severe that fruit size and weight are reduced considerably.

REARING PROCEDURE AND EQUIPMENT

The rearing procedure was begun by collecting eggs in the field. Leaves were cut from banana plants and the under surfaces examined for eggs. When an egg was located a small disk with the egg attached was cut from the leaf and placed in a petri dish. Soon after hatching, each small larva was placed in a separate petri dish on a disk of banana leaf that had been cut to fit the bottom of the dish. The disks were changed every 12 hours in order to measure the amount that had been eaten.

The larvae passed into the pupal stage in the petri dishes. After each molt the length of the larva and the diameter of the head capsules were measured. When pupation was complete the covers were removed from the petri dishes and the pupae placed in screen cages, where they remained until the adult moths emerged.

Small potted banana plants were placed in the cages to provide a place for oviposition for the adult moths. Eggs were deposited on the underside of the leaves of these small plants, but none of the eggs were observed to hatch. These eggs may not have been fertile, since copulation was not observed between male and female moths in the cages. In order to obtain fertilized eggs that would hatch it was necessary to collect female moths from the field and to place them in cages with small potted banana plants.

LIFE HISTORY AND HABITS

Oviposition.—Eggs are attached singly and in groups of 2 to 4 to the underside of young mature leaves. Oviposition by laboratory-reared female moths usually began on the second or third day after emergence. In no instance were more than 10 eggs deposited by any one of these moths. The abdomens of 20 female moths which emerged in the laboratory were opened and examined for

[1]Accepted for publication October 8, 1958.

[2]A subsidiary of United Fruit Company.

Table 1.—Observations made on 20 individuals over a period of one month.

Observations of each instar	Instars							Pupa	Total days egg to adult
	1	2	3	4	5	6	7		
Average no. of days in each stage—egg to adult	2.6	2.0	2.9	2.6	3.0	3.2	4.7	9.1	29.9
Average width in mm. of head capsules	0.43	0.58	0.78	1.09	1.60	2.21	3.09		
Average length in mm.	2.19	3.54	5.32	7.64	10.57	14.92	20.47		
Average leaf area eaten in mm.^{2}	17.25	33.7	131.85	277.35	751.7	2,174.1	5,144.05		

eggs. These moths were 2 to 5 days of age and had deposited no eggs. This examination revealed from 21 to 30 fully developed eggs in the abdomen of each moth. Examination of the abdomens of moths less than 2 days of age revealed a mass of undeveloped eggs. Fourteen female moths collected in the field and placed in cages with small banana plants deposited a total of 56 eggs. The greatest number of eggs deposited by any one of these moths was 15. The above information suggests that under normal conditions in the field the female can deposit upward of 30 eggs.

The Egg.—The egg (fig. 1) is subglobose, greenish in color, and averages 0.81 mm. in diameter. Approximately 24 hours before hatching, the color of the egg changes to milk-white and the reddish-brown mandibles of the larva become visible through the partially transparent egg shell. Movement of the mandibles, as the larva eats its way through the shell, can be detected 12 hours or more before the egg hatches.

Of the 56 fertilized eggs deposited in the laboratory by female moths, 38 hatched in 5 days and 18 hatched in 6 days; none failed to hatch.

In the field eggs are often parasitized by the hymenopterous parasite, *Trichogramma minutum* Riley. These parasitized eggs turn black 24 to 48 hours before the small parasites emerge, making them easy to detect.

The Larva.—Soon after emerging from the egg, the larva turns around and begins to eat the egg shell (fig. 2). If undisturbed, the larva consumes the shell in 4½ to 6 hours and thereafter begins to feed on the leaf near the place where the egg was attached. If disturbed while feeding on the egg shell, the larva will leave and will feed on the leaf without completely consuming the shell.

After each molt the larva partially or completely consumes its own exuviae before beginning to feed on the leaf again. The larva feeds mostly on the underside of the leaves, moving backwards and feeding parallel to the small veins (fig. 4). Because of their very small mouth parts, the first-, second-, and third-instar larvae eat only part way through the leaf. Older larvae, however, eat completely through the leaf, leaving holes as much as 3½ inches long and ½ to 1 inch wide.

In the field the entire larval life is spent on the under surface of the leaf. This is also true for larvae reared on small potted plants in the laboratory. When larvae were placed in petri dishes containing pieces of banana leaves they fed both from above and below the pieces of leaf and showed no preference for the upper or lower surface.

Ninety percent of reared larvae passed through seven instars and ten percent passed through only six instars.

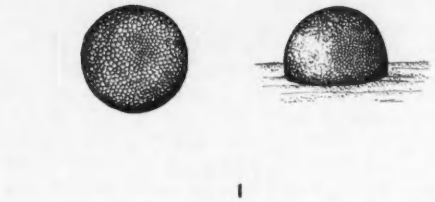
On the basis of rearing behavior, the duration of the first instar is from 2 to 4 days, whereas the average duration of each instar from the second through the sixth is only 2 to 3 days. The duration of the last instar, whether it be the sixth or the seventh, is the longest, averaging from 4 to 6 days.

The records on food consumption in table 1 show that in these tests the greatest amount of food was consumed by the last larval instar. In fact, the last instar consumed more food, i.e., destroyed more leaf surface, than all of the preceeding instars as a group.

Following the methods of Dyar (1890), measurements were made of the head diameter of each instar to detect each molt (table 1).

Following each molt, the length of each larva was recorded as shown in table 1. The ratio of head diameter to instar length of the larvae reared in the laboratory compared favorably with that of larvae collected in the field. Thus the amount of food consumed by the larvae in the laboratory is comparable to the amount consumed in the field.

The Pupa.—Pupation usually takes place on the under surface of the same leaf on which the larval life is passed, or behind the leaf sheaths on the side of the pseudostem. Pupae are often



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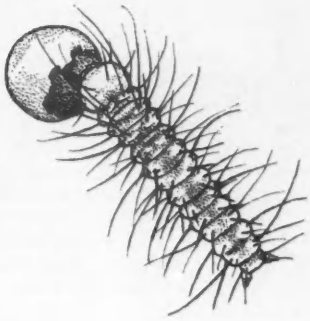

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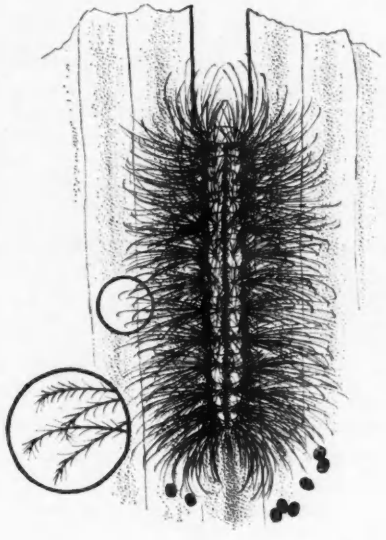

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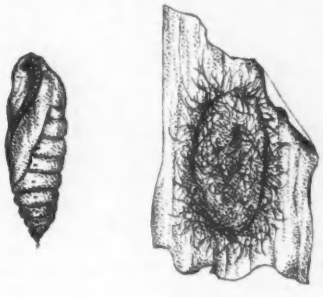

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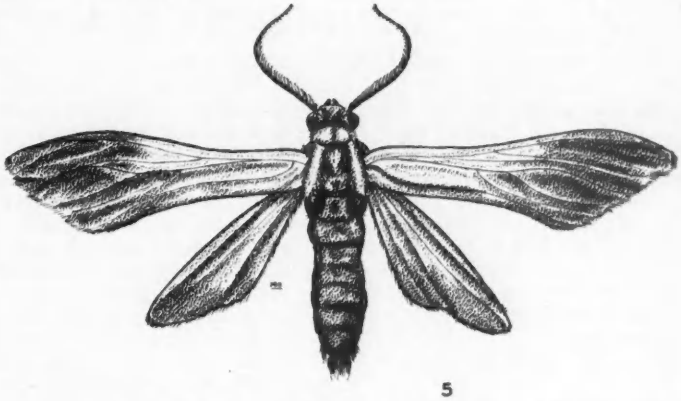

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FIG. 1.—Dorsal and lateral view of egg. FIG. 2.—Young larva feeding on egg shell. FIG. 3.—Seventh instar larva. FIG. 4.—Pupa and cocoon. FIG. 5.—Dorsal view of adult.

found, however, under the drying, curling tips of aging leaves.

The pupa is enclosed in a very thin, weak cocoon (fig. 4) which is made chiefly from the long, white hairs of the caterpillar. The pupal life of caterpillars reared in the laboratory varied from 8 to 10 days, although in one case the pupal life was 16 days.

The Adults.—The emergence of the adult from the cocoon is relatively rapid, requiring only a few minutes. In the laboratory the newly emerged adults climbed immediately onto the screen sides of the cages where they rested for some time. After an hour or more they began to fly about the cage but generally they remained stationary on the side of the cage or underneath the leaves of the caged plants.

The adult is a medium-sized bluish-black moth (fig. 5) with a wing expanse from 30 to 40 mm. A small tuft of brilliant red scales is located on each lateral surface of the prothorax. Male moths may be easily distinguished from female moths by the color of the front coxae, the ventral surfaces of which are covered with snow-white scales in the males. The front coxae of the females are uniformly blue-black in color.

The moths are very active during the day and often may be seen flying about in open sunny areas. In the laboratory the adults lived from 3 to 6 days. The short life was probably due to lack of proper food, since, on several occasions in the field, adults have been observed feeding on the blossoms of orange and lemon trees.

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NEW SPECIES AND STRAINS OF APHYTIS (HYMENOPTERA, EULOPHIDAE) PARASITIC ON THE CALIFORNIA RED SCALE, AONIDIELLA AURANTII (MASK.), IN THE ORIENT[1]

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ABSTRACT

This paper deals primarily with the *Aphytis* species or lesser categories considered to be definite and regular parasites of the California red scale, *Aonidiella aurantii* (Mask.), in the Orient. The importance of species of *Aphytis* as parasites of diaspine scale insects is discussed and the potential value of strains or other subspecific categories in biological control is emphasized. Pupal pigmentation is described for four species or groups and is shown to be of taxonomic importance. A key is given to five species (or forms) of Oriental *Aphytis* parasitic on the California red scale. Two new species, *Aphytis melinus* and *A. fisheri*, are described, as are two forms whose status is in doubt, the Assam form of *A. hispanicus* and the Kagoshima form of *A. citrinus*. The adult females of *A. melinus* and *A. fisheri* are very similar, if not indistinguishable, morphologically, but they do not interbreed and the pupae are quite distinct. The known distribution of these species in the Orient is given.

The great economic importance of the California red scale, *Aonidiella aurantii* (Mask.), as a pest of citrus in California and other parts of the world, has led to a considerable effort being expended on studies of and explorations for natural enemies. Until about 10 years ago *Aphytis chrysomphali* Mercet was considered by the leading specialists in biological control of the California red scale, as well as by the *Aphytis* taxonomists, to be the dominant if not the only *Aphytis* species attacking this scale (Compere, 1955).

Previous to 1948 the work of *Aphytis "chrysompahli"*[2] in biological control of the California red scale had received both adverse and favorable notice. In 1948 and subsequently DeBach and coworkers, studying the California red scale in certain completely untreated groves in southern California, proved through qualitative and quantitative experimental field population studies that *A. chrysomphali* was actually controlling the California red scale at very low population densities in certain groves or areas. This led to intensive studies on *Aphytis* by the author and coworkers, which have continued to the present time.

In 1947–48 S. E. Flanders received shipments of diaspine scales at Riverside from J. Linsley

[1]Paper No. 1097, University of California Citrus Experiment Station, Riverside California. Accepted for publication October 15, 1958.

[2]Other species may be involved under this name.

Gressitt in South China, which yielded an *Aphytis* whose pupa possessed a dark pigmented pattern not found in *chrysomphali* in California. This led Flanders to suspect that a different species was involved, so this form was cultured on the California red scale and widely colonized in southern California. It is now established and more abundant in some areas than *chrysomphali*. This second species of *Aphytis* known to be parasitic on the red scale was described as *A. lingnanensis* Comp. (Compere 1955).

Field studies in recent years have indicated that various species of *Aphytis* are of great value in controlling diaspine scale populations. As a whole, this genus seems to contain more than its share of efficient parasites. As already mentioned, *A. chrysomphali*, without the aid of other natural enemies, controls the red scale in certain groves or areas in southern California which have an environment favorable to the parasite. *A. lingnanensis* has demonstrated the same ability. Although two imported internal parasites, *Comperiella bifasciata* How. and *Prospaltella perniciosi* Tow., are well established in certain areas, neither has demonstrated that it has the ability to regulate red scale populations at low population densities. In the Orient my observations led to the carefully considered conclusion that in general *Aonidiella aurantii* was being maintained under very satisfactory natural control by natural enemies. The most widely distributed and most common enemy was *Aphytis* of one or more species. The occasional isolated tree, branch, or twig outbreaks of *Aonidiella aurantii* seen by me were nearly always associated with ants, and ants have been proven to produce this same result in California through adverse effects on natural enemies.

Aphytis mytilaspidis (LeB.) has been shown by Lord and MacPhee (1953) to produce good natural control of *Lepidosaphes ulmi* (L.) in the Annapolis Valley of Nova Scotia. *A. maculicornis* (Masi), introduced into California from Iran and Iraq against the olive scale, *Parlatoria oleae* Colvee, has been shown by Doutt (1953) to have caused reductions in scale populations of from 90 to 98.6 percent within 12 to 18 months. Doutt (1954) states: "Based upon the examination of the imported host material and the emergence of adult parasites it is apparent that the dominant parasitic enemies of *Parlatoria oleae* in its native range are species of the aphelinid genus *Aphytis*." *A. lingnanensis* from China is now rapidly reducing populations of the Florida red scale, *Chrysomphalus ficus* (Ashm.), in Israel and is showing definite promise of satisfactory biological control, according to correspondence I have had with I. Cohen. I observed *A. lingnanensis* to be the dominant parasite of the Florida red scale in the Orient.

Another Oriental *Aphytis*, *A. lepidosaphes* Comp., was introduced and colonized on the purple scale, *Lepidosaphes beckii* (Newm.), in southern California in 1948. It has spread throughout the purple-scale-infested area and has greatly reduced the outbreak potentialities of this scale. The Department of Biological Control at Riverside made shipments of *A. lepidosaphes* to Mexico, and E. Jimenez has informed me in correspondence that the purple scale is being greatly reduced in numbers as a result. Personal observations in the Orient showed *A. lepidosaphes* to be the dominant parasite of the purple scale, with its range extending from Formosa to the foothills of the Himalayas in North India. Additional observations in California and in many foreign countries have indicated that *Aphytis* species other than those previously mentioned are frequently the dominant parasites and controlling factors of various other species of diaspine scale insects.

Unfortunately, certain inherently efficient species of *Aphytis* are not so broadly adapted to as great a range of climatic variation as are their hosts. This has been illustrated by the work of Lord and MacPhee (1953) in Nova Scotia, where *A. mytilaspidis* controls its host in the Annapolis Valley but fails to do so in the colder central New Brunswick area, and by DeBach et al. (1955) in California, where *A. chrysomphali* and *A. lingnanensis* are severely limited in effectiveness by the colder winters and hotter summers of interior climatic areas.

If new species, or strains, of such imperfectly adapted species could be obtained from their hosts from new areas, chances for better biological control might be enhanced. Inasmuch as Compere (1955) has indicated that probably a great many more forms of *Aphytis* exist than have been described, it seems hopeful that new species or strains parasitic even on the most well-known diaspine scales may be discovered.

The author had this possibility in mind while engaged in foreign exploration for new natural enemies of the California red scale in the Orient during 1956–57, and in requesting the cooperation of Paul Oman and George Angalet of the United States Department of Agriculture in making shipments of parasitized red-scale material in 1955–56 from India.

Angalet's shipments resulted in one new species (*Aphytis melinus*) being obtained from the California red scale and cultured in Riverside in 1956. I obtained this same new species in Pakistan in 1957, and it was cultured in Riverside from my shipments also. These cultures were combined later, inasmuch as they interbred readily, and have since been widely colonized in the field. My shipments also resulted in another new species (*A. fisheri*) being obtained on the California red scale in Burma and cultured in California. A new form of *A. hispanicus* (Mercet) was obtained in Assam, where it was the dominant red-scale parasite around Gauhati, but

no parasites survived shipment. A very similar form was successfully sent from Burma and cultured on the California red and other diaspine scales in the insectary at Riverside. However, the host of this form is not definitely known. If it occurs on the red scale at all in Burma it is rare, because I never saw mottled *proclia*-type pupae in any of numerous dissections of thousands of California red scale in Burma. Also, a presumably new form, near *citrinus*, was found in Japan.

Based on the restrictions that time and geography imposed on the surveys and collections of Angalet and DeBach, it is likely that additional species or strains of *Aphytis* parasitic on California red scale in the Orient will be discovered.

SYSTEMATICS

In this paper, Compere's work on systematics of the genus *Aphytis* is being followed as the basic reference (see Compere 1955). Forms will be described herein which are not readily separable on the basis of adult morphology, but which are quite distinct biologically or as immatures. Because of the economic importance of this group it seems desirable that these differences should be pointed out and names applied, because considerable reference will be made to these forms in the literature.

The use of pupal pigmentation as a taxonomic character.—The degree and pattern of pigmentation of the pupal integument can be a great aid in determination of species or groups of species.

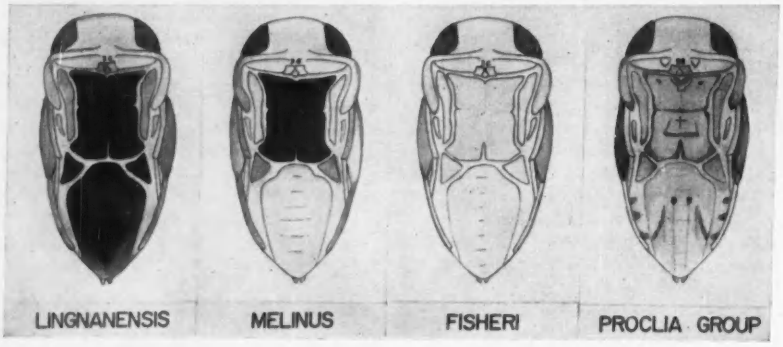

FIG. 1.—Four types of *Aphytis* pupae showing typical pigmentation.

In fact, further taxonomic studies of specimens already collected may disclose that some have already been found. The chances are that we now know the most common or dominant forms. At least we think we do. However, only 11 years ago we thought *A. chrysomphali* was the only *Aphytis* attacking red scale in the Orient. Then we obtained *A. lingnanensis* from China and Formosa. In the last 2 years we have obtained the four aforementioned new Oriental species or strains parasitic on the red scale, and it is now highly questionable that *chrysomphali* occurs in the Orient at all.

Aside from the Oriental forms, preliminary study of preserved specimens from South Africa indicates that *Aphytis chrysomphali*, as recorded in the literature, is not the only *Aphytis* species attacking the California red scale there. This further emphasizes the need for more detailed taxonomic study of *Aphytis* reared from the California red scale around the world and again points out the possibility of discovering new species or strains better adapted to some of the California citrus-growing areas than the ones we already have.

When such characters afford a reliable means of determination, binocular examination of field-collected material makes it possible to determine more accurately which forms are definitely parasitic on the California red scale or on any other given host. The collector, of course, must be able accurately to recognize the host scale in the field. If, however, adult parasites are merely reared from a lot of field-collected material, often more than one species of diaspine scale may be present, so it may be difficult to say positively which was the true host. Pupal examination also may enable the collector to evaluate the relative abundance of any given species with respect to another. In this paper only species considered to be definitely and regularly parasitic on the California red scale in the Orient are included. As already mentioned, we now have in the insectary an *Aphytis* (Burma *hispanicus*) that originated from four adult females and one male reared from a shipment of California red scale material from Maymyo, Burma, in February 1957. This form, which has the distinctive mottled pupae of the *proclia*-group (for species in *proclia*-group see Compere 1955), is being cul-

Table 1.—Pupal types of *Aphytis* found at each of 22 Oriental localities.

	lingnanensis	*citrinus*	*melinus*	*fisheri*	*proclia*-group
Japan					
Kagoshima		?		x	
Formosa					
Hsinpu	x				
Feng Hsan	x				
Taichung	x				
Puli	x				
Kao Hsiung				x	
Hong Kong					
New Territories	x				x
Thailand					
Bangkok	x			x	
Burma					
Rangoon	x			x	
Pegu	x				
Kalaw				x	
Heho	x			x	
Taunggyi	x				
Maymyo	x			x	
Kyaukme				x	
Bhamo				x	
India					
Gauhati	x				x
Saharanpur	x				
New Delhi			x		
West Pakistan					
Lahore	x		x		
Rawalpindi			x		
Haripur			x		

tured on and colonized on the California red scale in the field in southern California. However, intensive binocular microscope examination of thousands of *Aphytis* pupae throughout Burma never revealed a mottled pupa under a California red scale. Thus, I cannot consider this form to be a normal parasite of the California red scale in Burma. On the other hand, a very similar pupa was found to represent the dominant parasite of the California red scale around Gauhati, Assam, India.

Four more or less distinctive types of *Aphytis* pupae were found on the California red scale in the Oriental areas visited by me in 1956–57. No California red-scale-infested locality was checked unless one or more species of *Aphytis* was found on this scale. The four types of pupae may be best distinguished when in the mature, green-eyed stage. Typical pigmentation development may not have occurred in pupae that have reached only the red-eyed stage, and newly formed pupae in the white- or clear-eyed stage of development are too young to be used for this purpose. A description of the four pupal types follows; but it must be clearly understood that each type may include more than one species of *Aphytis* and that considerable variation within types may occur.

lingnanensis type: dark (shiny blackish), well-defined pigmentation on midthoracic sterna and on midventral abdominal plates; head, wing pads, and appendages usually yellow to yellow-brown; dorsal surface yellow.

melinus type: dark (blackish) pigmentation on midthoracic sterna, less well-defined than in *lingnanensis*; abdomen clear (yellowish) ventrally; head, wing pads, and appendages usually yellow; dorsal surface yellow.

fisheri type: thoracic and abdominal sterna and head clear (yellowish); wing pads and appendages may vary from yellow to yellow-brown; dorsal surface yellow; no black lines or furcae whatsoever on body.

proclia-group type: wing pads and appendages fuscous to black; dark areas or furcae visible on both dorsal and ventral surfaces of thorax and abdomen; abdominal segments with dark patches dorsolaterally; coarse, black spines evident.

Figure 1 shows a comparison between typical pupae of these four types.

The types of *Aphytis* pupae found in each of 22 localities were determined by careful examination with the binocular microscope. These data are summarized in table 1.

From this admittedly fragmentary study of the distribution of *Aphytis* pupal types certain indications may be noted. The *lingnanensis* type has the greatest distribution, extending from Formosa, where it is generally distributed, through South China and Thailand, across Burma and India to northwest India. Its range appears to end at about the border between northwest Pakistan and India. The *melinus* type was found only in northwest India and northwest Pakistan (southern areas were not surveyed).

Table 2.—Some differences between various forms of *Aphytis hispanicus* and *Aphytis diaspidis*

Form	No. of specimens checked	Characters								Sexuality
		No. of setae on mesoscutum		No. of setae on tergum no.						
				7[a]		8[a]		10[b]		
		Range	Av.	Range	Av.	Range	Av.	Range	Av.	
Assam *hispanicus*.... ex *Aonidiella aurantii*	11	11–17	14	2–3	2	4	4	10–14	12	Biparental
Burma *hispanicus*.... ex ?	11	11–16	12	3–5	4	6–9	7	9–11	10	Biparental
Hong Kong *hispanicus* ex *Aonidiella aurantii*?	10	11–13	11	2–4	3	6–7	6	7–9	8	Uniparental
Mexico *hispanicus*... ex *Parlatoria pergandii*	6	10–11	10	2–3	2	5–6	5	6–8	7	No males in collection
Texas *hispanicus*..... ex *Parlatoria pergandii*	4	10–14	12	3–5	4	6	6	8–9	8	No males in collection
California *diaspidis*.. ex *Hemiberlesia lataniae*	10	13–16	14	4–6	4	6–9	8	8–16	12	Uniparental

[a]Between lateral pigmented areas.

[b]In a curve between cerci.

The *fisheri* type appeared to center in Burma, with extensions eastward through Thailand (dominant form at Bangkok), Formosa (rare), and to Kagoshima, Japan. The *proclia*-group type was taken on California red scale only in Hong Kong (rare) and at Gauhati, Assam, India, where it was the commonest form. The "*citrinus* type?" listed for Kagoshima is discussed under the Kagoshima *Aphytis citrinus* Comp. Preliminary indications are that the *citrinus* type may resemble the *melinus* type in the pigmented pattern. Again I wish to emphasize that a given pupal type does not mean that only one species is involved under that type. It probably does indicate a degree of relationship, however.

Collections in the North Mediterranean area (Greece, Italy, Spain) did not reveal *lingnanensis*, *melinus*, or *fisheri* pupal types on the California red scale, the dictyospermum scale, *Chrysomphalus dictyospermi* (Morgan), the oleander scale, *Aspidiotus hederae* (Vallot), or any of the other diaspine scales examined. The *chrysomphali* type pupa was the only one seen on the California red scale in this area. It is nearly completely yellow but differs from the *fisheri* type in having a short definite black pigmented line between the midcoxae.

Pupae of the *proclia*-group type are of worldwide distribution on various hosts.

The pupae of *Aphytis lepidosaphes* might be mistaken for those of *chrysomphali* or *fisheri*; however, as far as is known, *lepidosaphes* only parasitizes the purple scale, *Lepidosaphes beckii*. The following description of the mature green-eyed pupa of *A. lepidosaphes* should distinguish it from the pupa of *A. fisheri* which has no dark markings, and the pupa of *A. chrysomphali* which has a single black line between the coxae of the mesosternum. The mature green-eyed pupa of *A. lepidosaphes* is, in general, golden yellow in color, with the head paler and the wing-pads darker. The most distinguishing character is a black, Y-shaped marking on the center of the mesosternum. There is also a less visible black, inverted T-shaped marking on the prosternum just posterior to the mouthparts, and a short, definite, black marginal line on either side of the center of the posterior margin of the scutellum.

Preparation of specimens.—Microscopic examination of most of the whole-mounted specimens studied in this report was made of individuals prepared by a new technique that is simple and generally superior to older methods. These preparations result in individuals having the body turgid and of normal shape, the wings undamaged, the body contents cleared and the integumental pigment generally unchanged. Slides made more than 2 years ago show no deterioration, but the ultimate keeping quality of such mounts is unknown. Old, dried specimens prepared by this method make excellent mounts. Typical preparation for dried specimens is as follows:

(1) Place specimens in glacial acetic acid and leave until body contents are more or less cleared and a lifelike turgidity obtained (usually no more than 30 to 60 minutes).

(2) Remove from acetic acid and place directly in a drop of Hoyer's mounting medium on a slide. Place cover slip over drop.

If live specimens are at hand, place in xylol for about 1 hour, then follow steps (1) and (2) above.

Many of the characters used in the present study would not be discernible on shrivelled whole-mounted specimens in balsam or other media.

KEY TO SOME SPECIES AND STRAINS OF APHYTIS PARASITIC ON THE CALIFORNIA RED SCALE IN THE ORIENT[2]

Adult Females

1. Cranium without black bars and margins; spines on head and thorax not coarse or black 2
   Cranium with black bars and margins; spines on head and thorax coarse and black; spines arising along anterior margin of lateral fuscous areas of abdominal terga; usually only two spines on tergum 7 and four spines on tergum 8 between lateral fuscous areas; 10 to 14 (usually 12) spines on tergum 10 between the cerci; basitarsus of middle and hind legs slightly fuscous; 11 to 17 setae on mesoscutum (usually 14) . . Assam form of **hispanicus**
2. Thoracic sterna usually with dusky areas . . . . . **lingnanensis**
   Thoracic sterna clear 3
3. Antennal club short and stout, no more than 3 times as long as wide, wing-fringe hairs long, one-fourth to one-third the width of the forewing; usually four sensilla on club . . . . Kagoshima form of **citrinus**
   Antennal club relatively long, 3½ to 4 times as long as wide; wing-fringe hairs about one-sixth to one-seventh the width of the forewing; usually five sensilla on club 4
4. Antennae relatively long and narrow, little increase in width of joints from scape to club; funicle joints 1 and 2 rounded, not compressed; pedicel distinctly longer than last funicle joint; 10 spines on mesoscutum; pupae pigmented on venter of thorax as in fig. 1 . . . . . **melinus**
   As above, except pupae without any distinct pigmented areas . . . . . **fisheri**

This key applies only to species or forms definitely known to be parasitic on the California red scale in the Orient. For a more general key to species and groups of *Aphytis* see Compere (1955).

DESCRIPTIONS

Aphytis hispanicus (Mercet): The Assam form.

Distinguishing characters.—The combination of characters given in the above key separate the Assam form from all other forms of *hispanicus* and *diaspidis* (How.) I have examined. Males common.

Provisionally, the Assam form is assigned to *hispanicus*; however, some major characters take this form to *hispanicus* and some to *diaspidis* in Compere's key (Compere, 1955). Pigmentation of the antennal club is like *hispanicus*, the length of the club is like *diaspidis*, the ratio of the greatest forewing width to the longest marginal fringe resembles *diaspidis*, the number of setae on the mesoscutum overlaps both species, the general coloration is perhaps more like *hispanicus* than *diaspidis*.

Aphytis hispanicus and *A. diaspidis*, as delimited by Compere (1955), either are extremely variable species or in fact they include a number of closely related but distinct species. Currently we do not know which is the case. Certainly, forms I have examined of *diaspidis* from California and Connecticut, and of *hispanicus* from Assam, Hong Kong, Burma, and Mexico, appear to be more distinct from each other than is the case with certain distinct but very similar and difficult-to-separate species such as *lingnanensis* and *lepidosaphes*. However, the more one examines *hispanicus* from different localities the more the overlapping and intergradation of characters become apparent, until it is questionable whether a certain form is *hispanicus* or *diaspidis* or perhaps, on the other hand, *maculicornis*.

The inclusion of the Assam red-scale-inhabiting form of "*hispanicus*" as *hispanicus* in this paper represents a compromise. I am convinced it is different than "standard" *hispanicus* from *Parlatoria pergandii* (Comst.), but this whole group, in fact the whole *proclia*-group, needs intensive study before *hispanicus* is split into more than one species.

Aphytis hispanicus (Assam form) is biparental, with males common. In life the males appear nearly yellow in contrast to the darker (grayish) females. This characteristic coloration of the males applies also to Connecticut *diaspidis* males. The Assam form was discovered by me in March 1957 to be the most common parasite of the California red scale, *Aonidiella aurantii*, in and around Gauhati, Assam, India. As far as I know, this is the only instance where a *hispanicus* or other *proclia*-group type has been found to be anything other than an incidental or rare parasite of the California red scale in nature. A shipment was made (Department of Biological Control S. & R. No. 1714) of this material from Gauhati to Riverside for culture and colonization on the California red scale in the field. Unfortunately, most of the parasites emerged and died en route, so no culture was possible. The adults from this shipment are preserved on two slides in the collection of the Department of Biological Control, University of California, Riverside. They bear the S. & R. No. 1714.

Aphytis hispanicus from Assam is not so generally or darkly pigmented nor are its spines generally so coarse and dark as *diaspidis* from California. However, it is more so than *hispanicus* from *Parlatoria pergandii* in Texas and Mexico. On the lateral pigmented areas of the abdominal terga there are usually two spines on each side of tergum 3, three spines on each side of tergum 4, four spines on each side of tergum 5, five spines on each side of tergum 6, and six spines on each side of tergum 7 (for tergal nomenclature see Compere, 1955, fig. 1).

[2]For morphological terminology relating to *Aphytis* in this key and the following descriptions and discussions see Compere (1955).

Aphytis hispanicus from Hong Kong seems to have about the same number of spines in the lateral pigmented areas of the abdomen, but the spines originate along the anterior margin of the pigmented areas in the Assam *hispanicus* and within the pigmented areas in the China *hispanicus*. A similar form from Burma, but which probably does not occur on the California red scale in nature, usually has more lateral spines on terga 6 and 7.

A comparison of what seem to be fairly stable differences between the various forms examined is made in table 2, which indicates that there are probably distinct differences between the forms examined, although only a few individuals of each were studied. The Assam *hispanicus* is the most distinct form of all. The presence of only four setae on tergum 8 alone distinguishes it from the others. The usual occurrence of only two setae on tergum 7 between the lateral pigmented areas separates it most of the time from all other forms except the Mexico *hispanicus* and perhaps the Hong Kong *hispanicus*. The relatively large number of setae (10 to 14, average 12) on tergum 8 between the cerci distinguishes the Assam *hispanicus* from all others but the California *diaspidis* and sometimes the Burma *hispanicus*. The combinations of characters given in the table usually should enable each form to be distinguished from the others, except perhaps the Burma *hispanicus* from the Texas *hispanicus* or the latter from the Mexico *hispanicus*.

Little knowledge exists regarding the distribution of the Assam form. I collected only around Gauhati, Assam. However, various field observations and shipments from northwest India and northwest Pakistan failed to reveal any evidence of *hispanicus* on *Aonidiella aurantii*.

The Hong Kong *hispanicus* was obtained and cultured in the insectary at Riverside from three females that issued from *Aonidiella aurantii* material collected on pummelo trees by S. K. Cheng at Sek Po, Hong Kong, New Territories, May 1–6, 1955. It was shipped to the Department of Biological Control under S. & R. No. 1457. It was cultured on *Hemiberlesia rapax* (Comst.) for one generation and then subsequently reared on California red scale and colonized in limited numbers in the field. It is not absolutely certain that the three original females came from the California red scale, because a few specimens of other scale species could have been present. However, the fact that I observed some *proclia*-type pupae on California red scale in the field at Hong Kong (New Territories) and that this form was propagated on the California red scale in our insectary, strongly indicates that this is the form that sometimes occurs on the California red scale in South China. It differs from the Assam form as shown in the previous discussion.

Aphytis lingnanensis Compere

Aphytis lingnanensis has been described and its distinguishing characters pointed out by Compere (1955). In the collection of the Department of Biological Control at Riverside are numbers of slides referred to this species from South China and Formosa. On my trip to the Orient in 1956–57 I obtained many specimens which were referred to *lingnanensis* or *lingnanensis*? by H. Compere. These came from the following countries or areas and usually from *Aonidiella aurantii*: Hawaii, Formosa, Hong Kong, Thailand, Burma, and India. This distribution agrees closely with that shown previously for *lingnanensis*-type pupae.

Probably various forms—possibly different species—are now included under the name *lingnanensis*. Of the various shipments sent in from India during 1956–57, only one *lingnanensis* type was cultured at Riverside because priority was being given to new species. This *lingnanensis* originated from *Aonidiella orientalis* (Newst.) on rose at Khunti, India (near New Delhi), and both the pupae and adults are inseparable, as far as we know, from typical *lingnanensis*. It is cultured readily on *Aonidiella aurantii* in the insectary. However, this "Khunti" *lingnanensis* fails to cross with typical *lingnanensis* from China, Hawaii, or Mexico (which cross freely with each other) except very rarely and then the F_1 hybrids are sterile. It differs from typical *lingnanensis* in various biological characteristics. To all intents and purposes the "Khunti" *Aphytis* is not *lingnanensis*, but it will be considered such pending further study. How many other similar biological forms exist within the range of so-called *lingnanensis* is anybody's guess. This form is being colonized on *Aonidiella aurantii* in southern California.

Aphytis citrinus Compere: The Kagoshima form.

Aphytis citrinus has been described and its distinguishing characters pointed out by Compere (1955).

I obtained specimens which run to *citrinus* in Compere's key (Compere 1955) at Kagoshima, Japan, November 15, 1956, by beating citrus trees heavily infested with *Aonidiella aurantii*. Other diaspine scales were scarce on these trees. *Aphytis* adults were abundant and consisted of two species, each about equally common. These were sent to Riverside under S. & R. No. 1655, but none survived shipment.

Binocular examination of material collected from these trees showed two types of *Aphytis* pupae common on *Aonidiella aurantii*—a *fisheri* type and a type which I described in field notes as having "weak *lingnanensis*-type pupal pigmentation." These, I now think, were the pupae of the Kagoshima *citrinus* inasmuch as *citrinus* pupae I have since examined in California

would fit this description. Although this does not constitute definite proof that *citrinus* is parasitic on *A. aurantii* at Kagoshima, the circumstantial evidence is very strong.

This is the only record I know that *citrinus* is a parasite of *Aonidiella aurantii*, except for several definite, but fairly unusual, recent rearings of *citrinus* from *A. aurantii* in southern California. Compere (1955) considered *citrinus* to be parasitic only on yellow scale, *Aonidiella citrina* (Coq.). The Kagoshima *citrinus* is biparental. Some of the males possess distinctive, black-tipped middle tibiae, and there are similar, but fainter, markings on certain females.

The Kagoshima *citrinus* does not agree in detail with specimens of *citrinus* from California. It has relatively long and pale setae on the thorax compared to the California form, 8 to 10 setae across terga 7 and 8 as compared to 4 to 6 setae for the California form, usually 10 setae on the mesoscutum as compared to 8 for the California form, and the heavy spines of the outer row on the costal margin of the forewing are about twice as long as the spines of the inner row, whereas in the California form the spines of each row are about equal in length. However, in view of Compere's discussion (Compere 1955, pp. 312–3) regarding the lack of knowledge concerning true relationships between *Aphytis citrinus*, *A. dubius* De Santis, and *A. aonidiae* (Mercet), the Kagoshima form will be considered to be *citrinus* for the present. Eventually it may prove to be a distinct species.

Aphytis melinus, new species

Distinguishing characters.—Large size. Body of female wholly yellowish, no fuscous areas or furcal pigmentation. Antennae long and slender, with only a slight taper from scape to end of club. Club nearly four times as long as wide. Pedicel distinctly longer than last funicle joint; first and second funicle joints roundish, not compressed. Scape about as long as pedicel and funicle joints combined, club somewhat shorter. Five sensilla on club, one on last funicle joint. Ten setae on mesoscutum. Posterior margin of propodeum with large overlapping crenulae. Longest front wing-fringe hairs short, slightly, if any, longer than spines on costal margin. Mature pupae with black pigmented thoracic sternal plates as shown in figure 1. A biparental species, with males common. Males like females in color, and without dusky markings or lines. Venter of male abdomen with microscopic stippling.

In Compere's key (1955) *Aphytis melinus* would run to either *cylindratus* Comp. or *lingnanensis*. Without proper mounts so that the crenulae on the posterior margin of the propodeum could be seen, it could also run to *immaculatus* Comp. *A. cylindratus* differs from *melinus* in that the club is longer (over four times as long as wide) than in *melinus*, the club is distinctly longer than the scape, the pedicel is shorter than the third funicle joint, the first and second funicle joints are compressed and the crenulae (four pairs) on the posterior margin of the propodeum in *cylindratus* do not overlap.

Aphytis lingnanensis differs most obviously from *melinus* in having dusky thoracic sterna. The club is also shorter and the pupae differ as shown in figure 1.

Aphytis immaculatus resembles *melinus* superficially; however, it has more setae on the mesoscutum (12 or more) than *melinus* (usually 10), the antennae are shorter and more clubshaped, joints 1 and 2 of the funicle are compressed and closely appressed, and the club is shorter (no more than three times as long as wide). *A. immaculatus* also possesses small, uncrowded crenulae on the posterior margin of the propodeum.

Extensive laboratory mating tests have shown that *Aphytis melinus* will not cross with *A. lingnanensis*, *A. lepidosaphes*, *A. fisheri*, or the "Khunti" *lingnanensis*. No other species crosses have been tried, but *fisheri* is undoubtedly its closest relative.

Aphytis melinus was first received in the insectary of the Department of Biological Control at Riverside on September 12, 1956. One hundred and eight females and twenty-seven males emerged from *Aonidiella aurantii* collected by G. W. Angalet on rose at New Delhi, India, September 5, 1956. Original data are recorded under S. & R. No. 1643 of the Department of Biological Control, Citrus Experiment Station, Riverside. Dr. T. W. Fisher successfully cultured this material in quarantine. Angalet made two more shipments of *Aonidiella aurantii* on rose, which also gave rise to cultures of *Aphytis melinus*. These came from Lahore, Pakistan, September 16, 1956 (S. & R. No. 1646), and from Gurgaon, India, October 26, 1956 (S. & R. No. 1651). A fourth culture was obtained from a shipment (S. & R. No. 1737) sent by me from Saidpur Village (near Rawalpindi), West Pakistan, April 3, 1957. These parasites were collected on the yellow scale, *Aonidiella citrina*, on orange and pummelo.

Mating tests showed that all four of these cultures (New Delhi, Lahore, Gurgaon, and Saidpur Village [=Culture "P"]) crossed readily and produced normal sex ratios and numbers of progeny. They were therefore combined into one mixed culture which has been massproduced in the insectary, and nearly 2,000,000 adults have been colonized on *Aonidiella aurantii* on citrus during 1957 and 1958. Numerous field recoveries have been made through July 1958.

Types of *Aphytis melinus* are to be deposited in the U. S. National Museum, and paratypes in the British Museum and in the collection of the Department of Biological Control, University of California at Riverside. Two slides bearing 20

to 30 adults of both sexes, as well as some pupae mounted in Hoyer's medium, will be deposited in each institution. These specimens represent parasites reared in the insectary at Riverside on *Aspidiotus hederae*, an insectary host. They came originally from a mixed culture which combined individuals received from New Delhi and Gurgaon, India, and Lahore and Saidpur Village, West Pakistan, as set forth in the preceding two paragraphs.

Aphytis fisheri, new species

Distinguishing characters.—Adult characters virtually identical with those given for ***melinus***. Setae or spines more evident on ***fisheri*** at same magnifications. Mature pupae differ from the pupae of all other species I have observed in being completely yellowish, with no blackish sternal plates, lines, or furcae (figure 1). A biparental species, with males common. Will not cross with ***melinus***.

Aphytis fisheri is being described as a new species because it will not cross with ***melinus***, the species it most closely resembles, because its pupae are distinctive, and because comparative tests have shown that it differs in biological responses such as fecundity, longevity, and temperature tolerance from ***melinus***, ***lingnanensis***, and ***chrysomphali***.

Aphytis fisheri was first noticed by me in the field December 21–22, 1956, on ***Aonidiella aurantii*** on pummelo and rose at Kalaw and Taunggyi, South Shan States, Burma, on the basis of having wholly yellow mature pupae. A shipment (S. & R. No. 1673) of ***Aonidiella aurantii*** on rose collected December 21–25 at Taunggyi and Heho, South Shan States, Burma, yielded four female and two male ***fisheri*** in the insectary at Riverside. These few were successfully cultured in quarantine by T. W. Fisher, after whom this species is named. Subsequently (1957–58) mass culture and field colonization on ***Aonidiella aurantii*** has been carried on by the author and coworkers throughout southern California. Some field recoveries have been made.

Aphytis fisheri coexists in about equal numbers with ***lingnanensis*** on ***Aonidiella aurantii*** throughout Burma. No ***melinus***-type pupae were seen by me in Burma, nor were ***fisheri***-type pupae seen in India or Pakistan.

Thus far we have found no significant morphological differences between adults of ***fisheri*** and ***melinus***. Morphological distinction between the two is now more of an art than a science, and not a very well-developed art at that. Some characters that help to differentiate the two species are:

A. melinis	**A. fisheri**
Hairs on edge of hind wing from hamulae to the wing-tip (to first long wing-tip hair) nearly equal in length.	Hairs on edge of hind wing from hamulae to wing-tip (to first long wing-tip hair) decreasing noticeably in length from hamulae to tip.
The two long hairs at apex of the hind wing about 2 times as long as hairs on leading edge just before the apex.	The two long hairs at apex of the hind wing about 2.5 to 3 times as long as hairs on leading edge just before the apex.
6–8 pale spines evident on mesoscutum at 45x magnification (dissection binocular).	10 spines evident on mesoscutum at 45x magnification (dissection binocular).
Greatest hind-wing width about 1.1 to 1.5 times that of the longest fringe hairs.	Greatest hind-wing width about 1.5 to 2 times that of the longest fringe hairs.
Spines on male notum indistinct at 45x magnification.	Spines on male notum distinct at 45x magnification.

Types of ***Aphytis fisheri*** are to be deposited in the U. S. National Museum, and paratypes in the British Museum and in the collection of the Department of Biological Control, University of California at Riverside. Two slides bearing 20 to 30 adults of both sexes, as well as some pupae mounted in Hoyer's medium, will be deposited in each institution. These specimens were reared in the insectary at Riverside on ***Aspidiotus hederae***, an insectary host. They came originally from four female and two male parasites collected on ***Aonidiella aurantii*** in Burma and were sent to Riverside for culture as set forth above.

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THE JAPYGIDAE (DIPLURA) OF NORTH AMERICA, 3. OCCASJAPYX SILVESTRI AND HECAJAPYX N. GEN.[1]

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ABSTRACT

Descriptions of the male of *O. californicus* Silv. and both sexes of *O.* **sierrensis** follow a redescription of the genus *Occasjapyx*. *Hecajapyx* is allied to *Occasjapyx*; its type species, *H.* **vulgaris**, has been found in seven California counties north of San Francisco. Types of both new species are in the California Academy of Sciences.

Members of the genera *Occasjapyx* and *Hecajapyx* in North America can be recognized by the following characteristics: absence of plumose body setae, antennae with 24 segments, first lamina of lacinia falciform, posterolateral angles of abdominal tergite VII projected to the rear, forceps asymmetrical with two prominent teeth on each arm.

The genus *Occasjapyx* was established by Silvestri (1948) with *Japyx americanus* MacGillivray as the type. In this paper he described *O. californicus* from three females and reported the male as unknown. He also included *Japyx kofoidi* Silv. (1928) in the genus *Occasjapyx*. Paclt (1957) placed five species of *Japyx* from Japan and four species of *Japyx* from China in the genus *Occasjapyx*, but did not give his reasons for doing so. These Oriental species will need to be carefully studied to determine if they are correctly placed in *Occasjapyx*.

This paper described the male of *O. californicus* Silv., a new species, *O. sierrensis* L. M. Smith, and a new genus and species *Hecajapyx vulgaris* L. M. Smith.

Genus **Occasjapyx** Silvestri

Antenna with 24 segments, first lamina of lacinia falciform and 4 pectinate laminae, terminal antennal segment about twice as long as broad. Thorax: pronotum 5+5M, mesonotum prescutum 1+1M and many microsetae, scutum 5+5M; metanotum as in mesonotum. Legs: setae at dorsal apex of femur 3M+1m+1M, tibia with setae more numerous apically, of which two ventral setae are thicker than the others, tarsi with 5 to 7 large ventral setae per row. Abdomen: tergite I: prescutum 2M, scutum 2M, tergite II: 3+3M plus 2 long subanterior submedian m; tergites III to VII 6+6M and two submedian subanterior m which become gradually shorter from the third to the sixth, and very short or absent on the seventh tergite; posterior corners of the second tergite rounded, of the third and fourth tergites obtuse, fifth tergite acute, sixth projected to the rear, and seventh strongly extended posteriorly and inwardly. Tenth tergite: L/W=1.1 approximately, carinae sclerotized and strongly convergent to the rear, with 2+2M between the carinae. First sternite with lateral subcoxal organs occupying four-fifths of the distance between the styli, composed of one to three rows of glandular setae and one row of shorter and thinner sensory setae, median subcoxal area with two groups of 5 to 10 short setae on either side of the median line, disculi absent in median line. Stylus with visible secondary cone, one straight seta one-third as long as the stylus, and one basad pore.

Female genitalia: two papillae anterior to orifice, two papillae posterior to orifice, about 8 tactile setae and 6 shorter sensory setae on each papilla, a slightly raised area at either side of orifice bearing 5 to 20 short sensory setae each. Male genitalia: a large lobe posterior to orifice with many minute setae on inner surface and fewer large setae on outer surface. A pair of papillae laterad to orifice, skewed-cone in shape, L: W=1.33 approximately, with short setae mesad and long setae laterad, and 5 to 10 small sensory setae in an irregular line from base to tip of palpus on the anterior face.

Right forceps arm with one premedial and one post-medial tooth, predental tubercles 3, interdental tubercles biserrate $\frac{5-10}{5-10}$, post-dental tubercles as crenulations 5–12. Left forceps arm with two premedial teeth or one may be postmedial, predental tubercles 3–4, interdental tubercles 5–8, postdental tubercles as crenulations 10–25.

Occasjapyx californicus Silv.

Male.—Antenna with 24 segments, last segment length 0.21 mm., width 0.08 mm., with two placoid sensillae ventral and premedial, none on penultimate segment; antennal segment VI width 0.31 mm., longest seta on antennal segment VI 0.63 mm.; labial palpus strongly tapered toward tip, length 0.31 mm., width at base 0.10 mm.; first lamina of lacinia falciform; lateral edge of galea with 4 setae, thumb of galea slightly sclerotized, broadly rounded at tip, with 5 to 10 long sensory cones; dorsum of head with about 24 long setae. Thorax: pronotum with 5+5M, meso and meta notum prescutum 1+1M and scutum 5+5M, tibiae with setae more numerous apically and two or three ventral setae stouter than the rest, tarsi tapering apically, metatarsus

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length 0.68, width at base 0.15 mm., tarsal claws subequal, empodium straight, sclerotized, one-third as long as longest tarsal claw, dorsal setae at apex of femur reading from anterior to posterior three long, one short, and one long. Abdomen: tergite I 1+1M and a pair of anterior median M which diminish on each successive segment and are absent on tergite VII, tergite II 3+3M and a pair of anterior median M, tergites III and IV 6+6M and a median pair of M, tergites V same as IV but with latero-median pair of setae reduced, tergite VI 5+5M with median pair and latero-median pair reduced to m, tergite VII 5+5M with both pairs of m absent, tergite VIII 2+2M, tergite IX 3+3m, tergite X with 2+2M between carinae, acropygidium slightly protruding, rounded. Lateral subcoxal organs with three rows of glandular setae and one row of sensory setae as long as the glandular setae, median subcoxal organ with 7+8 setae similar to sensory setae of the lateral subcoxal organs arranged in groups on either side of the median line, small median area without disculi or setae. Setose sacs in abdominal segments absent. Genital orifice oval, 0.28 mm. wide, with a thin membranous anterior flap bearing 4+4 large setae and 4+4 smaller setae, orifice ringed with a disorderly arrangement of about 50 microsetae, a large crescentic posterior flap bearing about 18+18 large setae; at either side of genital orifice a conical papilla bearing laterad eleven large setae and mesad about 20 smaller setae, papilla length 0.16 mm., width at base 0.14 mm., papilla 0.60 times the length of stylus VII. Pleuron V anterior pleurite with 3 microsetae, posterior pleurite with 2M, 1m, and 12 microsetae. Sternite I: prescutum 4+4M, scutum 13+1+13M and many m more numerous posteriorly, sternites II to VII with 16+1+16M with median seta becoming larger on each posterior sternite, sternite VIII 7+7M. Forceps: left arm with premedian and postmedian tooth, $\frac{11}{}$ predental tubercles 3, interdental tubercles —, $\frac{12}{}$ postdental margin smooth; right arm with two premedial teeth, predental tubercles 3, interdental tubercles 4, postdental tubercles (crenulations) 28.

Length of body including forceps 18 to 20 mm.

Described from four males collected with eight females in Mendocino County, California, by Mr. J. R. Helfer, in soil and humus.

Occasjapyx sierrensis, new species

Female.—Head: dorsum with about 14+14M, antenna with 24 segments, last segment length 0.11 mm., width 0.07 mm. with 2 median placoid sensillae and one premedian, second segment with one placoid sensillum, antennal segment VI width 0.20 mm., length of longest seta on VI 0.27 mm., labial palpus tapered, length 0.16 mm., width at base 0.06 mm., first lamina of lacinia falciform, lateral edge of galea with 2 setae. Other structures as in *californicus*, except metatarsus length 0.34 mm., width at base 0.08 mm., anterior median setae on abdominal tergites diminish on each succeeding segment and are absent on segment VII, latero-median setae not reduced, but full size on tergite VII; lateral subcoxal organs with one row of glandular setae and one row of shorter sensory setae, median subcoxal area with 5+5 setae, genitalia: one pair of papillae anterior to genital orifice and one pair posterior, anterior pair each with three setae and one sensory seta near the tip, at either side of the genital orifice a cluster of 8 small sensory setae. Abdominal sternite I: prescutum 4+4M and 3+3m, scutum 13+1+13M and many m more numerous posteriorly, sternites II to VII 16+16M, median M absent, sternite VIII 7+7M. Forceps: left arm with one premedian and one postmedian tooth, $\frac{7}{}$ predental tubercles 3, interdental tubercles —, $\frac{9}{}$ postdental tubercles 7; right arm with one premedian and one postmedian tooth, predental tubercles 3, interdental tubercles 6, postdental tubercles 13.

Length of body including forceps 10.5 to 14.0 mm.

Male.—Similar to female except genitalia, anterior flap not visible, width of genital orifice 0.18 mm., posterior flap with about 16+16 long setae, papilla with 8 long setae laterad and about 15 smaller setae mesad, and 4 short sensory setae, papillae length 0.140 mm., width at base 0.100 mm., papillae 1.2 times length of stylus VII. Sacs opening on abdominal segments III and IV containing 12+12 plumose setae in segment III and 8+8 plumose setae in segment IV. (These sacs may contain as few as one plumose seta in young males.)

Length of body including forceps 11.0 to 20 mm.

Habitat.—Type ♀, 2 paratype ♀♀ and 3 paratype ♂♂ 4 miles west of Newcastle, California, March 21, 1958, by L. M. Smith and R. O. Schuster; 3 paratype ♀♀ and 4 paratype ♂♂ same place, April 15, 1958, by L. M. Smith and R. O. Schuster, mostly 2 to 3 inches deep in loam soil; one paratype ♀, Folsom Lake, Placer County, Calif., May 2, 1958, under oak trees by W. H. Lange, R. James and W. Crites; two paratype ♀♀ and two paratype ♂♂, 3 miles north of Nashville, El Dorado County, Calif., April 25, 1958, in soil, by L. M. Smith and R. O. Schuster.

Type in California Academy of Sciences; paratypes in U. S. National Museum, California Insect Survey, University of California at Davis, and the author's collections.

This species is similar to *O. californicus* Silv. but is distinguished by the fact that the latero-anterior setae on the terga are not markedly

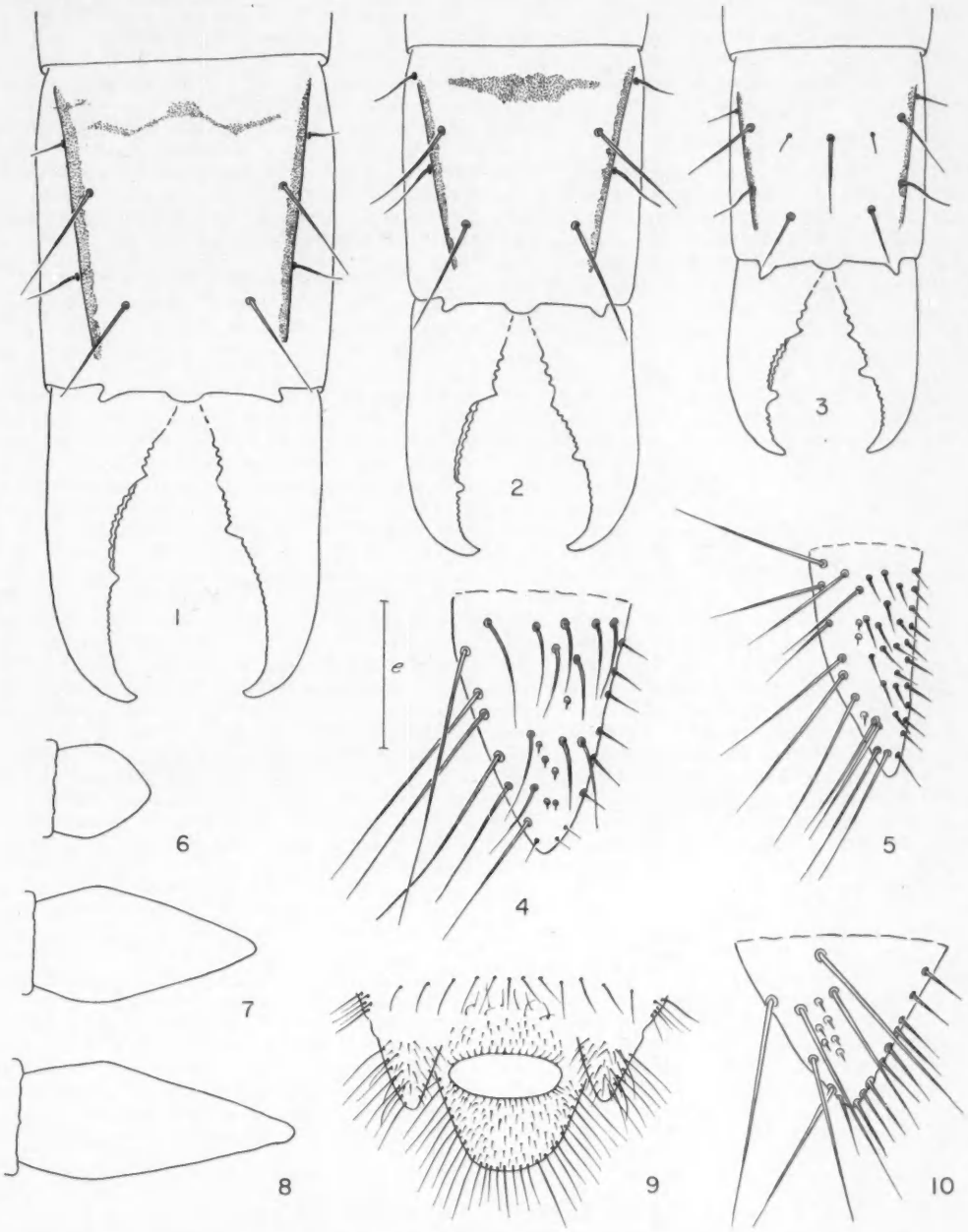


FIG. 1.—*Occasjapyx californicus* Silv., ♀, dorsal view of 10th abdominal segment and forceps, showing lack of median setae; e=0.75 mm. FIG. 2.—*O. sierrensis* L. M. Smith, ♀, e=0.5 mm. FIG. 3.—*Hecajapyx vulgaris* L. M. Smith, ♀, e=0.5 mm. FIG. 4.—*O. sierrensis*, ♂, genital papilla, anterior surface, e=0.1 mm. FIG. 5.—*H. vulgaris*, ♂, genital papilla; e=0.1 mm. FIG. 6.—*H. vulgaris*, ♀, last segment of antenna, dorsal view, setae omitted; e=0.1 mm. FIG. 7.—*O. sierrensis*, ♀, last segment of antennae; e=0.1 mm. FIG. 8.—*O. californicus*, ♀, last segment of antenna; e=0.1 mm. FIG. 9.—*O. sierrensis*, ♂, genitalia; e=0.5 mm. FIG. 10.—*O. californicus*, ♂, genital papilla; e=0.1 mm.

reduced caudad and are conspicuous on tergite VII; by the dentition of the forceps; by the smaller body size; by the single row of glandular setae in the lateral subcoxal organs; and no median seta on the sternites.

Hecajapyx, new genus

Female.—Head about as wide as long, with about 16+16 large setae, labrum emarginate with about 6+6 large basal setae and numerous smaller setae, antennae with 24 segments, terminal segment L: W = 1.0, with two placoid sensillae, first lamina of lacinia falciform, two-thirds as long as the second lamina, mandible with 5 teeth, external edge of galea with two short setae, thumb of galea broadly rounded at tip, bearing about 8 sensory cones, labial palpi tapered, L: W = 2.3, with about 7 long setae and three shorter setae, pronotum 5+5M and about 9+9m, mesonotum prescutum 1+1M, scutum 5+5M, metanotum same as mesonotum, abdominal tergite I 3+3M, tergite II 4+4M, tergite III through VII one pair median anterior setae, the same size on each segment, plus 6+6M, tergite VIII 2+2M, tergite IX 3+3m only, tergite X 3+3M between the dorsal carinae and one median M, acropygidium small and rounded, posterolateral angles of abdominal terga of segsegments I through VI rounded, segment VII angles projected to the rear, legs moderately long, dorsal setae at apex of femur, from anterior to posterior 3M,1m, and 1M, tibia with setae more numerous apically, of which two ventral setae are much stouter than the others, tarsi tapered, L: W = 3.5, tarsal claws unequal with anterior claw half as long as posterior claw, large ventral setae per row on tarsus 3 to 5, lateral subcoxal organs occupying seven-eights of the distance between styli, one row of glandular setae and one row of shorter sensory setae, median subcoxal area blank, styli with secondary cone not distinct, bearing one stout seta and nearby pore, genital orifice with a pair of anterior and a pair of posterior papillae each with numerous long setae and a few short sensory setae, laterad of genital orifice a slightly raised setose area bearing a cluster of 5 to 10 short sensory setae. Forceps: left arm with one premedian and one larger postmedian tooth with interdental margin bidentate, right arm with one premedian tooth and one larger postmedian tooth.

Male.—Similar to female except genital orifice oval, bordered posteriorly by uniform row of small sense setae on a large setose flap, genital papillae elongate cones L: W = 2.9, male setose sacs in abdominal segments III and IV absent.

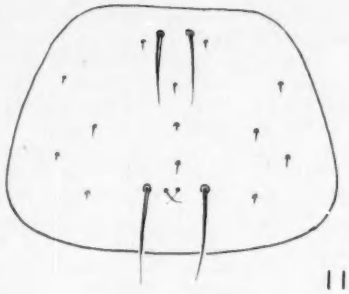
This genus is similar to *Occasjapyx* but differs as follows: Median subcoxal organ absent, terminal antennal segment almost spherical, abdominal tergite I with 3+3M, tergite X 3+3M between carinae, and posterolateral angles of terga I through V rounded.

Hecajapyx vulgaris, new species

Female.—Antenna with 24 segments, terminal segment length 0.06 mm., width 0.06 mm., two premedian ventral placoid sensillae, width of antennal segment VI 0.15 mm., length of longest seta on antennal segment VI 0.28 mm., labial palpi length 0.19 mm., width at base 0.064 mm., with seven long and four short setae, thumb of galea slightly sclerotized and broadly rounded at tip with nine sensory cones, two equal setae on external edge of galea, slightly longer than the sclerotized part of the thumb, pronotum with 5+5M and 8+8m with 2 m in the anterior row of M well developed, mesonotum prescutum with 1+1M, 4+4m and about 20+20 microsetae, scutum with 5+5M and about 20+20m, metanotum same as mesonotum, abdominal tergite I with 3+3M, tergite II 4+4M, tergites III–IX typical, tergite X with median lateral setae of the dorsum wavy, arising in sclerotization of carinae, pleuron IV anterior pleurite with one medium and one small seta, posterior pleurite with one long, one medium, and six short setae. Lateral subcoxal organs practically meeting in the midline, one row of glandular setae 34+37 with lateral setae slightly longer than mesad setae, laterad setae/stylus I = 0.7, one row sensory setae 35+37, laterad sensory seta/stylus I = 0.4. Styli (st) and seta on stylus (s): $s_1/s_7 = 0.77$; $st_1/st_7 = 0.69$; $s_1/st_1 = 0.63$, $s_1/st_7 = 0.43$. Median subcoxal organ absent. Sternite I: prescutum with 4+4M and 5+5m; scutum 14+14M and about 25+25m, not increasing in density toward the posterior margin of the scutum; sternites II to VII with 16+16M and numerous m, sternite VIII with 7+7M, anterior genital papillae with numerous long setae and an irregular row of 5 small sense setae with cluster of 4 sense setae near the tip, raised area on either side of genital opening with

EXPLANATION OF PLATE II

FIG. 11.—*O. sierrensis*, ♀, first abdominal tergite, showing lack of median pair of M; e = 0.5 mm. FIG. 12.—*H. vulgaris*, ♀, first abdominal tergite; e = 0.5 mm. FIG. 13.—*O. californicus*, ♀, dorsal view of posterolateral angles of abdominal tergites II to VII; e = 1.0 mm. FIG. 14.—The same for *O. sierrensis*, ♀; e = 1.0 mm. FIG. 15.—The same for *H. vulgaris*, ♀; e = 1.0 mm. Fig. 16.—*O. californicus*, ♀, median subcoxal organ and a portion of lateral subcoxal organ, ventral view, showing three rows of glandular setae; e = 0.13 mm. FIG. 17.—The same for *O. sierrensis*, ♀, showing one row of glandular setae; e = 0.13 mm. FIG. 18.—The same for *H. vulgaris*, ♀, showing absence of median subcoxal organ; e = 0.13 mm. FIG. 19.—*O. sierrensis*, ♀, third abdominal tergite, showing median anterior pair of setae and their reduction on tergites IV, V, and VI, and their absence on tergite VII; e = 1.0 mm. FIG. 20.—Third abdominal segment of *H. vulgaris*, showing median anterior pair of setae and their relative size on segments IV through VII; e = 1.0 mm.



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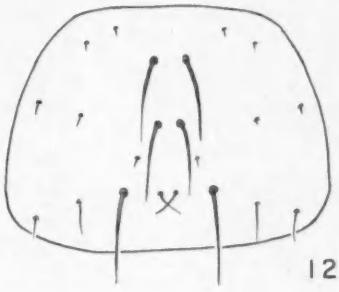

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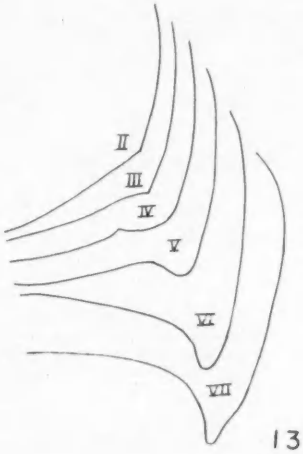

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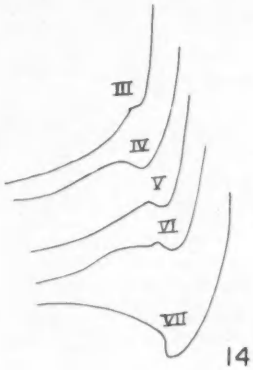

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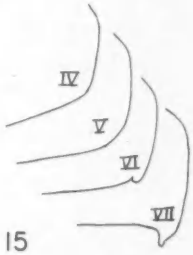

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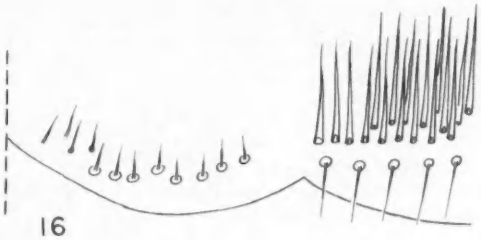

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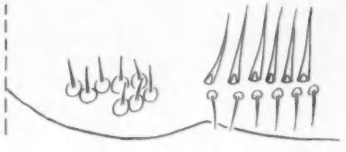

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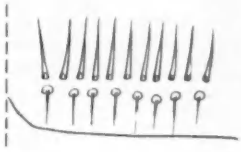

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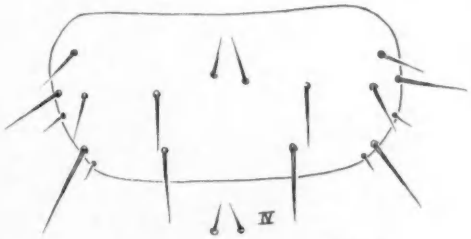

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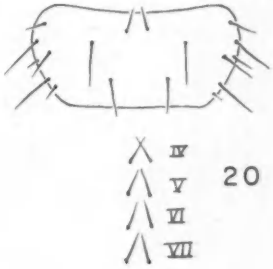

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8 to 10 small sense setae in a cluster; rectum without setae; forceps as illustrated, r=0.313.

Male similar to female except genital orifice oval with large posterior, semicircular flap, genital papillae slightly anterior to genital orifice, papilla 1.7 times the length of stylus VII.

Length of body including forceps 10.0 to 12.0 mm.

Habitat.—Type ♀, 5 paratype ♀♀, and 4 paratype ♂♂, San Anselmo, Marin Co., California, December 21, 1957, in oak duff and 3 inches of surface soil by Edna Smith; 7 paratype ♀♀ and 3 paratype ♂♂, 7 miles west of Oakville, Napa Co., California, Dec. 13, 1957, in redwood duff, by L. M. Smith and R. O. Schuster. One hundred and two other specimens collected in Del Norte Co., Sonoma Co., Lake Co., Mendocino Co., Solano Co., and Napa Co., California by various collectors.

Type in California Academy of Sciences; paratypes in U. S. National Museum, California Insect Survey, University of California at Davis, and the author's collections.

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APHID DISPERSAL OVER SOUTHERN CALIFORNIA DESERTS[1]

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ABSTRACT

Aphids that must have come from the irrigated valleys were trapped in isolated areas of the Colorado and Mojave deserts. Potted alfalfa plants set out in the same area as the traps on the Colorado desert caught an average of two aphids each in a week. Enough aphids were caught in every location to have infested fields planted there. The number caught indicated that aphids disperse across desert barriers.

The discovery of the spotted alfalfa aphid *Therioaphis* (*Pterocallidium*) *maculata* (Buckton) in irrigated valleys in desert southern California in June 1954 presented an opportunity to study the spread of a newly introduced insect and its effect on the ecology of the area. The spread of this insect had been, and continued to be, undeterred by considerable natural barriers. It is probable that this aphid was carried unwittingly by man over some of the more formidable barriers, but it also spread to all alfalfa in its path so inexorably that it seemed that natural dispersal must be taking place.

It has been known for some time that aphids and other light-bodied insects may be carried long distances by the wind. In 1827 and again in 1924 British arctic expeditions found live spruce aphids and syrphid flies landing on the snow in or near Spitzbergen. This followed a high wind from the direction of the nearest spruce forests on the Kola peninsula, 800 miles away (Elton 1925). The northward movement of the greenbug, *Toxoptera* (*Schizaphis*) *graminum* (Rond.) each summer through the grain belt in midwestern United States usually seems to occur by short hops, but Webster and Phillips (1912) reported a sudden northward jump by swarms of greenbugs in 1907.

In the spring of 1956, the author stopped to look at a stunted alfalfa plant growing beside a dried-up rainwater pool 4 miles south of Quartzsite, Arizona, and found it infested by spotted alfalfa aphid. This plant was 16 miles from the nearest alfalfa field.

During dry years the deserts of southern California are completely devoid of annual plants that can serve as hosts for many aphid species. This makes it certain that any aphid of any of these species taken out on the desert must have come from one of the irrigated valleys. It was decided to place aphid traps on the desert to see if aphids were dispersing over them.

METHODS

A trap consisted of a post set in the ground with two horizontal arms nailed to it and two yellow-painted sticky boards hung by wires between the arms. The yellow boards were 5 x 10 inches in size and were covered by tree-banding material which caught and preserved any small insect that flew against it. The boards were replaced weekly; the exposed ones taken to the laboratory and the aphids caught on them (or an

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aliquot) removed, washed in chloroform, cleared in a solution based on lactic acid, and identified.

It was decided to express the number of aphids dispersing through the district sampled as the number passing a 1-mile front. The sticky boards occupied only 100 sq. in. of space and therefore sampled only this area plus some additional area of air from which they attracted aphids. The boards were assumed to have caught four times the number of aphids passing through an equal area of air, a figure obtained by Dickson et al. (1956) in their work with citrus aphids. It was also assumed that aphid density was constant to 50 feet and that none occurred above that height. This is probably an underestimate (See Hardy and Milne 1938, Freeman 1945, and Johnson and Penman 1951), but was used to give a conservative figure. By calculation, a factor was obtained that, when multiplied by the average catch per trap, would give a figure showing the number of aphids passing a 1-mile front during the period that the trap had been exposed.

COLORADO DESERT, 1956

Five trap locations were set up on the Colorado desert on March 29, 1956, and maintained for 26 days. This area is a low desert averaging about 3.5 inches of rainfall annually. Vegetation is primarily creosote bush, *Larrea tridentata* Cov., mixed with some perennial saltbushes. There are trees, chiefly palo verde, *Cercidium floridum* Benth., and desert ironwood, *Olneya tesota* Gray, along the washes. At the time these traps were set out there had been little rain for some time so that there was no annual vegetation present.

The traps were placed roughly in a line, about 4 miles apart from Glamis to Midway Well, Imperial County. Irrigated farm land is located in three directions from the trap locations. The Imperial Valley lies to the southwest, its nearest edge 15 miles from the nearest trap location and 31 miles from the farthest one. The Yuma district is to the southeast, 27 to 33 miles from the traps, and the Palo Verde Valley to the north-northeast, 17 to 34 miles distant.

Sixteen species of aphids were caught, eleven that must have come from irrigated farms and five that could have come from the desert vegetation. In all, 199 specimens were caught, 186 of species that must have come from the irrigated land. This indicated a flight of about 3.5 million aphids from the irrigated area passing a 1-mile front during this 26-day period. Of these, 40.32 percent, or about 1.4 million were spotted alfalfa aphid. The green peach aphid made up 17.2 percent of the total, or an indicated 608,000 passing a 1-mile front.

There was no evidence of higher catches on the traps that were nearer any of the cultivated districts. This might have been expected since at this season of the year the light breezes, that normally carry the most aphids, were entirely variable. Only the high winds had a prevailing direction, from the northwest, and these generally carry few aphids. The trap location that made the highest catches was the one that was farthest from any irrigated land, 25 miles from the Palo Verde, 26 miles from the Imperial, and 29 miles from the Yuma Valleys. This was true for the spotted alfalfa aphid, for the green peach aphid, and for the total catch. The whole desert was covered by an immense floating population of aphids carried out from the irrigated valleys.

Experiments with potted alfalfa plants in these locations will be described in a later section.

MOJAVE DESERT, 1956

Once it had been shown that the Colorado desert was covered with flying aphids, the traps were moved to the Mojave desert, farther from cultivation. On May 1 five traps were set up in the area between Danby and Bagdad, in San Bernardino County, along Highway 66 between Barstow and Needles. The trap nearest to cultivated land was 57 miles distant and the farthest trap was 70 miles from any farm. The flora here is dominated by the creosote bush, but there is a greater variety of desert perennials than on the Colorado Desert. Recent seasons had been dry so annual vegetation was entirely absent.

The season was getting late for aphids in the desert valleys, so only 18 specimens from the irrigated valleys were caught during the 28 days that the five traps were exposed. These belonged to nine species and included two spotted alfalfa aphids and three green peach aphids. The total catch indicated about 235,000 aphids from cultivated land passing a 1-mile front during this 4-week period. Of particular interest was a single specimen of the sweetclover aphid, *Therioaphis* (*Myzocallidium*) *riehmi* Börner, caught during the period May 1 to 9. This species had just extended its range to include at least some of the irrigated valleys in desert California and Arizona, but was not yet present in readily discoverable populations in some of them. The trap on which it was caught was near Danby, about ½ mile north of the highway. This aphid must have blown in from the Coachella Valley, 78 miles to the south, or from Las Vegas, Nevada, 107 miles to the north. This catch probably illustrates how this imported aphid spread over the entire United States between 1948, when it was first found in New England, and 1956.

MOJAVE DESERT, 1957

On March 22, 1957, twelve traps were set out between Danby and Bagdad in the same area trapped in May, 1956. There had been practically no rain during the previous year, so that there was still no annual vegetation in the area. Exposed traps were replaced weekly until June 5, 1957, or for 75 days.

During this period, the 12 traps caught 1,051 aphids that must have come from the irrigated valleys and 1,303 that could have come from desert vegetation. The former included 16 species and the latter seven species.

That spring the spotted alfalfa aphid did not build up a high population in the desert valleys, so only three were caught in May. The most numerous species from the cultivated area was the apple grain aphid, *Rhopalosiphum fitchii* (Sand.), with 66.8 percent of the total. The green peach aphid was second with 20.4 percent and the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), third with 6.2 percent. Five aphid species that breed on grain crops contributed a total of 74.3 percent of the catch. An aphid, *Anuraphis* (*Sappaphis*) *inculta* (Walk.), which breeds only on carrot when found in desert valleys, made up 0.5 percent of the catch.

Aphids caught that could have come from desert plants were 98.2 percent cowpea aphid, *Aphis medicaginis* Koch. The second most numerous desert species was the saltbush aphid, *Aphis tetrapteralis* Ckll., with 1.1 percent. Both of these species will sometimes breed on creosote bush. Part of the catch of these two species undoubtedly came from the irrigated valleys.

Catches recorded by weeks (fig. 1) show that they rose to a peak on the week of April 11 to 18 and then dropped off sharply. This is an accurate story, although the previous week probably would have shown a higher catch than it did had there not been 4 days of high wind during that period. Not only does high wind prevent aphid flight, but sticky traps are coated with sand so that they become ineffective. The week of April 11 to 18 was free from high winds. The week of April 18 to 25 was windy while the following week was again relatively calm, but the main aphid flight from the irrigated valleys had ceased by then.

The population of aphids possibly from desert vegetation did not drop off as sharply as did that from the irrigated area. Aphids breeding on the desert would be less susceptible to predator attack than those in the irrigated area because of their wide dispersal. Also, the desert population was mostly cowpea aphid which breeds more rapidly at high temperatures than most aphid species.

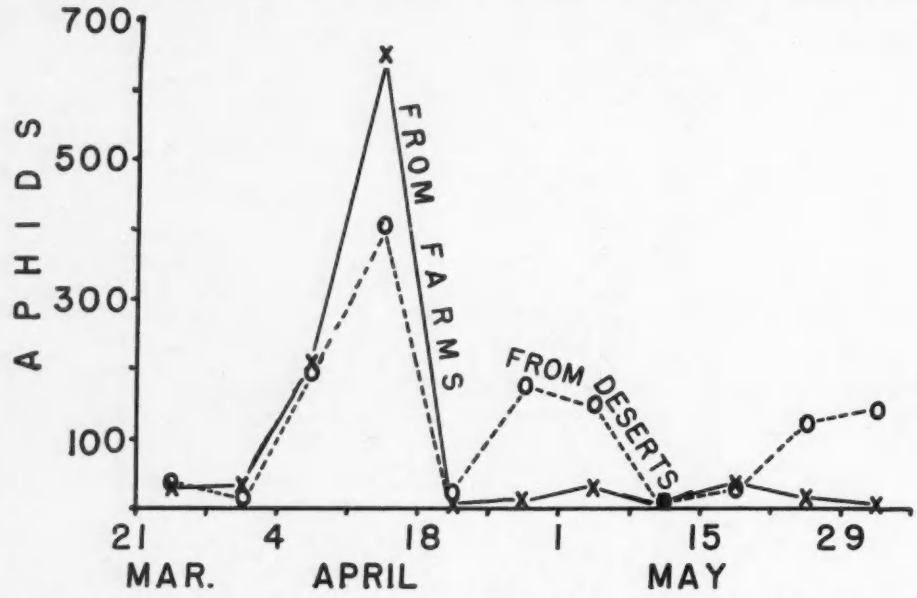

FIG. 1.—Total aphid catch each week on 12 traps exposed on the Mojave Desert in 1957. Aphids from irrigated valleys are shown separately from those that might have bred on the desert.

POTTED ALFALFA PLANTS

During the final week that traps were maintained on the Colorado Desert (April 17–24, 1956) seven alfalfa plants in pots were exposed adjacent to the three most remote traps, two by each of two traps, and three by the third. These plants had been grown in the greenhouse in 6-inch clay pots and were about 1 foot high. The pots were set into the soil so that their rims were at ground level. The dry period previous to this time had reduced the rodent population so that no plants were gnawed.

During the 7-day exposure, the seven alfalfa plants were infested by 14 alate spotted alfalfa aphids. Every plant was found by at least one spotted alfalfa aphid, and one plant caught six.

Nymphs were not counted except as evidence that at least one alata had been there. During the same period the plants were infested by four pea aphids, *Macrosiphum pisi* (Kalt.), and one cowpea aphid.

The three sticky traps exposed during the same period adjacent to the potted plants caught 18 spotted alfalfa aphids, no pea aphids, and 2 cowpea aphids. From this it can be guessed that a trap is about twice as effective as an alfalfa plant is catching alfalfa-infesting aphids, and that one sticky board is about equal to an alfalfa plant.

DISCUSSION

The figure of 8.8 million aphids from the irrigated valleys passing a 1-mile front in the isolated part of the Mojave Desert in 1957, while of considerable size, does not actually show a large aphid flight, when compared to those sometimes encountered in farming areas. The author once exposed a single 5 x 10-inch sticky trap for 60 seconds during a heavy aphid flight near Brawley, California and caught about 700 green peach aphids on it. The aphids were swarming out of a sugar beet field about 2 miles from the trap. Calculated as explained above, this indicated a flight of about 133 million aphids passing a 1-mile front each minute, or 23,940 million passing during the 3-hour period that the heavy flight lasted that afternoon.

If it is assumed that the 8.8 million aphids passing the 1-mile front in the Mojave Desert over the 11 weeks had landed on a farm 1 mile square there would have been less than 14,000 per acre or one aphid per 3.16 sq. ft. (0.294 sq. meters). This contrasts with figures from the heavy flight near Brawley of 37 million for each acre of the hypothetical farm (859 per sq. ft. or one aphid per 0.167 sq. in.) during the single 3-hour flight. This calculates out to about 6,000 aphids for each cantaloupe plant on the farm while actual observation showed that each cantaloupe plant in an actual field was visited by about 9,000 green peach aphids during the 3-hour flight (Dickson et al. 1949).

Of the total indicated flight on the Mojave Desert in 1957, aphid species infesting grain made up 6.2 million, the green peach aphid 1.7 million and spotted alfalfa aphid 23,000; all calculated as passing a 1-mile front. These would have infested each acre of the hypothetical 640-acre farm with 9,634 grain aphids, 2,648 green peach aphids, and 37 spotted alfalfa aphids. These aphids would have provided the start of an infestation, but numbers were very small when compared with flights of greenbug, *Toxoptera* (*Schizaphis*) *graminum* (Rond). as reported by Webster and Phillips (1912).

The traps on the Colorado Desert in 1956 indicated a flight of 1.4 million spotted alfalfa aphids passing a 1-mile front during the 26-day period sampled. This would have seeded a 1-mile square alfalfa field, if one had been there, with 2,227 of these aphids per acre, or about one aphid for each 50 alfalfa plants. This would not have caused immediate damage, but a 1,400-fold increase, which could have occurred in three generations even in the presence of a moderate population of predators, would have brought the spotted alfalfa aphid up to the threshold of economic damage at the level of 40 aphids per stem.

The seven potted alfalfa plants "caught" 14 spotted alfalfa aphids during the 7 days they were exposed. During this same period the traps caught aphids that indicated 532,000 of this species passing a 1-mile front, or one aphid for each 131 alfalfa plants in a 640-acre field. Two aphids found each potted alfalfa plant, on the average, or 262 times the allotment on a space basis. This may give some measure of the searching that goes on in an area of host scarcity.

The infestation of the alfalfa plants showed conclusively that aphids from the irrigated valleys were arriving in isolated desert areas alive and in condition to reproduce. This was further indicated by the observation that some specimens of species from the irrigated farms caught on the traps were still alive when the traps were visited.

No green citrus aphid, *Aphis spiraecola* Patch, was taken on the desert even though this species was in large population on the coast during the trapping periods. It does not breed on the desert, except to a limited extent on spiraea recently imported from the coast. The Mojave Desert location was 77 miles (airline) from the nearest infested citrus while the Colorado Desert location was 115 miles away. High mountains lie between the coastal citrus districts and the desert, and these may have prevented green citrus aphids from reaching the traps.

It would appear from these trap records that quarantine barriers of 5 or 10 miles are completely ineffective against insects that disperse readily, as aphids do. Even a barrier of 75 miles will be inadequate unless it is helped by such natural barriers as high mountains, or prevailing contrary winds.

It appears that a great deal of the spread of the recently introduced spotted alfalfa aphid was by natural dispersal and that this same dispersal pattern will continue. It would seem that an aphid population through a season is not limited to a field or a township but may cover several states.

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DISPERSAL OF ADULT HIPPELATES PUSIO, THE EYE GNAT[1]

RICHARD P. DOW

ABSTRACT

Female eye gnats maintained on honey in the laboratory retained more than half their original radioactivity 5 days after being tagged with P^{32}. When tagged gnats were released at the center of three concentric circles of traps on a windy day, some moved 25 feet directly upwind but an equally large number was caught 75 feet downwind in traps on the outermost circle, on both sides of the mean downwind direction. Releases of tagged gnats ½ and 1 mile from a rural population center in southwestern Georgia resulted in almost complete penetration of the small town on the day of release. In one test, traps more than a mile from the release box caught 15 gnats in less than 3½ hours after it was opened. Chi-square analysis was used to test the hypothesis that tagged gnats are distributed like the wild ones. Local departures from an overall equilibrium between tagged and untagged gnats could be recognized, and progress of the dispersal could be followed by comparing successive collections.

The oviposition of *Hippelates pusio* Loew, the eye gnat, takes place in freshly turned soil, and the larvae are widely distributed in cultivated ground. When soil insecticides were found effective in controlling the immature stages (Dow and Willis, 1959), it became advisable to learn if they also would provide a means of controlling adult gnats on an areal basis, for instance, in a small rural town. The first question needing an answer was how far from an area to be protected would it be necessary to extend the application of soil insecticide.

Preliminary studies of the flight behavior of *Hippelates* showed that little or no information could be obtained by trapping gnats whose place of origin was unknown. The release and recapture of marked specimens seemed to be an absolute necessity for the conduct of productive tests. Attempts to use fluorescent dyes to tag adult gnats met with difficulties similar to those described by Thomas (1951). Accordingly, with the aid of the Technical Development Laboratories of the Communicable Disease Center in Savannah, Georgia, tests were made on the use of radioactive phosphorus, P^{32}, as a tagging material. This work was done under the guidance of Mr. Jens A. Jensen and with his active collaboration.

TEST OF METHOD OF RADIOACTIVE TAGGING

Procedure.—Bait-trap collections of *Hippelates* made in southwest Georgia were sorted into three 1-quart fruit jars, and fed on different concentrations of P^{32}, as phosphoric acid, in diluted honey. The radioactive solution was offered in 2 ways: 0.1 ml. on a piece of paper, and 0.1 ml. on a microscope slide (the more acceptable). The P^{32} was introduced in the jars between 2 and 2:30 p.m. on the day after trapping. Specimens removed from these jars 20 to 21 hours later were anesthetized with CO_2 and placed in separate cells in which they could be maintained individually.

These ingenious holding cells, devised by the Technical Development Laboratories, are made by boring holes, 1 cm. in diameter, near the margins of handy-sized pieces of heavy illustration board, about 2 mm. thick. On one side, the holes are sealed with strips of cotton cloth (batiste), stapled and taped to the cardboard. On the other side, each cell is covered with a piece of thin, transparent plastic (polystyrene), so taped to the cardboard that it can be raised and lowered like a trap door. The flies are introduced on this side but are fed with a honey solution applied to the cloth on the other side.

In the afternoon of the second day after trapping, the radioactivity of the *Hippelates* was measured with a Tracerlab Model SU-3 laboratory monitor. The end of the G-M tube, shielded by a tubular metal extension, was about 1¼ inches from the holding cells and the readings were made through the polystyrene windows. The 5- and 10-day readings were not made until the gnats had been transferred to clean and previously unused holding cells.

Results.—Since nearly all of the marked speci-

[1]From the Communicable Disease Center, Bureau of State Services, Public Health Service, U. S. Department of Health, Education, and Welfare, Greeley, Colorado. Accepted for publication November 4, 1958.

mens in the holding cells were found to be females of *H. pusio*, the outcome of the tests is described with reference to these specimens alone. The mortality for the whole period of 10 days was only 26 percent and there was no indication of a difference related to the concentrations of P^{32}. Only one individual had an initial level of radioactivity so low as to suggest either no feeding or an error in reading the monitor (50 c.p.m., not corrected for background activity). The maximum (19,450 c.p.m., corrected for background) was in a specimen fed on the most concentrated solution of P^{32}. In 5 days there was an average decrease in radioactivity to 61 percent of the original readings, and in 10 days to 41 percent of the original readings (table 1, fig. 1). This is consistent with observations made by Jensen and Fay (1951) on three species of muscoid flies that also were maintained on diluted honey: *Musca domestica* L., *Callitroga macellaria* (F.), and *Phaenicia pallescens* (Shannon).

Table 1.—Radioactivity (counts per minute, corrected for background) of adult female *H. pusio* after overnight feeding on honey solutions that contained 3 different concentrations of P^{32} and after 5 and 10 days of maintenance on non-radioactive honey solutions.

Microcuries per ml. of sol.	No. of *H. pusio*	Mean c.p.m. per *H. pusio*		
		0 days	5 days	10 days
400	17	10,860	6,560	4,600
100	26	2,380	1,390	910
25	20	700	500	190

Discussion.—When Jensen and Fay maintained tagged muscoid flies on whole milk, the decrease in radioactivity was quite rapid (fig. 1), presumably because milk contains a much higher concentration of phosphorus and its abundance in the diet permitted its replacement in the tissues. This test was not conducted with *H. pusio*, but the fact that the eye gnat probably obtains

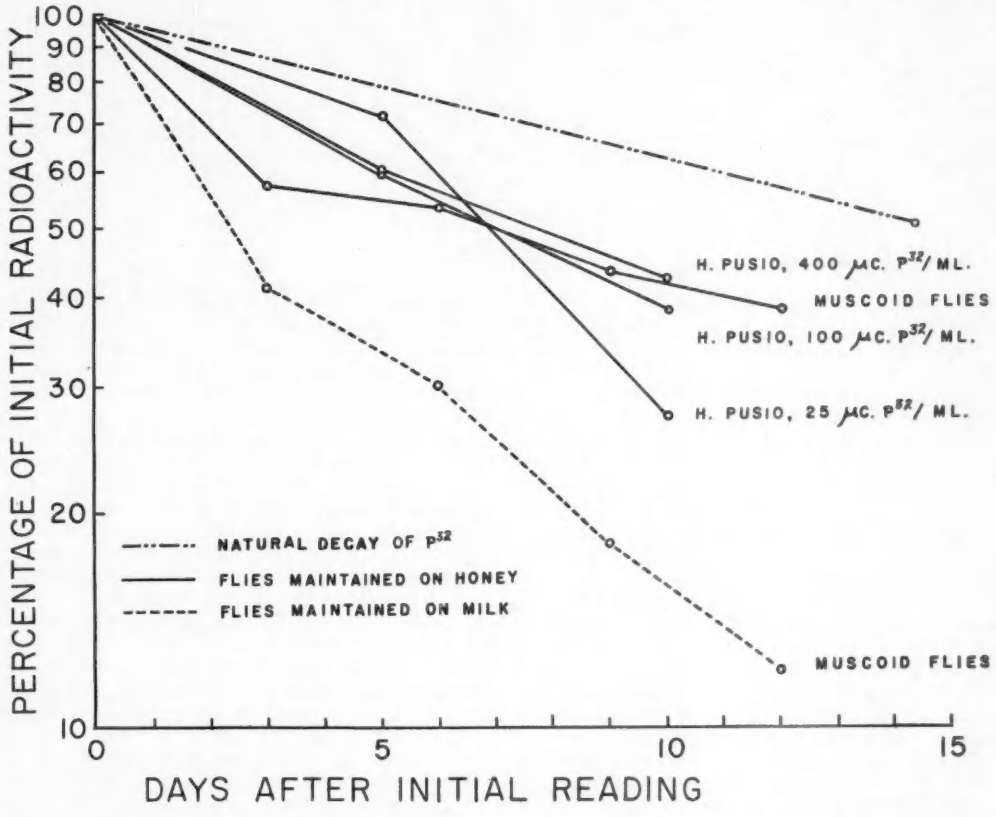

FIG. 1.—Loss of radioactivity in flies tagged with P^{32}. Original data on female *H. pusio*, fed overnight on the three indicated concentrations of P^{32} in honey, and maintained on honey, are compared with data from Jensen and Fay (1951) on female muscoid flies (*Musca domestica*, *Phaenicia pallescens*, and *Callitroga macellaria*), fed 2 and 3 days on milk containing 1 microcurie P^{32}/ml., and maintained on either honey or milk.

phosphorus whenever it feeds on such substances as sweat and secretions of the eye suggests that, when marked and released under field conditions, *H. pusio* will lose P^{32} at least as rapidly as the muscoid flies maintained on milk in the laboratory. Another reason for taking a cautious attitude toward the retention of P^{32} in released flies is the much greater scope of activity which they are permitted in nature.

TEST OF RECOVERY AT SHORT RANGE

Purpose.—Before undertaking a full-scale release experiment on the effective flight range of *H. pusio*, it seemed advisable to determine whether gnats fed on P^{32} in honey solution could be recaptured in traps baited with putrefied liver in the immediate vicinity of the release point. It was hoped that the attractiveness of the trap bait for gnats would not be affected by their having fed previously on honey. Another objective was to study the flight of *H. pusio* with respect to wind direction.

Procedure.—The area selected for the short-range recovery test was a slightly sloping field covered with low grass and weeds. It was located in an unused part of the Municipal Airport at Thomasville, Georgia, where it was remote from both farming and residential sections. The traps were arranged in three concentric circles around the release point (figure 2). They were 5 feet apart on the circumference of the outermost circle (radius 76.4 ft.), 10 ft. apart on the circumference of the middle circle (radius 50.9 ft.), and 20 ft. apart on the circumference of the innermost circle (radius 25.5 ft.).

An estimated 9500 *Hippelates* collected in traps baited with putrefied liver were fed on 14 ml. of a 1:1 honey and water mixture containing P^{32} in a quantity sufficient to provide 100 microcuries of activity for each ml. of solution. The gnats were fed in a special holding and release box, 18 x 18 x 18 inches, with glass windows on all four sides and an opening in the top with a sliding metal cover. A hole was dug at the release point so that the top of the box would be flush with the surface of the ground.

Though the radioactive honey was offered to the gnats on August 23, 1952, and everything was ready for their release the following morning, the weather was unusually cold and windy and there was some rain. The release was therefore postponed and did not take place until August 26 at 5:35 a.m., just after all the traps had been freshly baited. Sunrise was at 6:08 a.m. Between the release and the time that afternoon when the first collections were removed from the traps (3:30 to 3:50 p.m.), 39 estimates of the mean wind direction and its range during observation gave a grand mean of northeast (E 38° N) with mean limits of NNE (N 19° E) and E (E 6° N) and extreme limits of NNW (N 15° W) clockwise to SSE (S 30° E). Similar observations on the wind velocity gave a grand mean of 8 miles per hour with mean limits of 5.9 to 10.3 m.p.h. and extreme limits of 1.9 to 14.8 m.p.h. The air temperature, measured by sling psychrometer, rose gradually from 64° to 89° F. (at 1:50 p.m.) and dropped slightly thereafter.

A second collection in each trap was made during the period between 4 p.m. on the day of release and the following afternoon, and a third collection between then and 3:30 p.m. on the third day of the test. The bait poured on day 1 was used on all three days. Throughout this period the prevailing winds blew from the northeast, but before the end of the test their velocity had diminished greatly.

Table 2.—Recovery, by sector and by distance from release point, of tagged *H. pusio* on day 1 of the short-range recovery test.

Distance from release point	No. of traps in each sector	Direction of sector from release point								Total tagged *H. pusio*
		NE	E	SE	S	SW	W	NW	N	
25.5 ft.	1	12	2	1	3	5	3	2	2	30
50.9 ft.	4	1	0	2	2	3	1	0	1	10
76.4 ft.	12	0	1	1	12	5	12	2	1	34

Results.—Ninety-five radioactive *Hippelates* were recovered on day 1, five on day 2, and none on day 3. The specimens taken on day 1 were all females but only 74 were *H. pusio*. The remainder consisted of 21 *H. bishoppi*, too few to warrant analysis, but with a distribution apparently like that of the radioactive *H. pusio*.

The recoveries of tagged *H. pusio* on day 1 show a very definite orientation with respect to the strong northeast wind (table 2). The largest number in any trap, 12, was taken upwind in the nearest circle; in the outermost circle, the largest concentrations were downwind. This occurrence suggests that, as the tagged *H. pusio* left the release box, many responded to the attractant odor coming from the northeast and attempted to fly upwind to reach its source, also that those failing to do so were mostly swept downwind. With respect to the effect of wind, it is interesting to summarize some observations made in Jamaica by H. W. Kumm (1935) on *Hippelates flavipes*

Loew. An average of 534 specimens per man per catch was taken at wind velocities from 0 to 300 feet per minute; an average of 44 per man per catch was taken at wind velocities from 301 to 700 feet per minute; and no specimens were caught at wind velocities exceeding 700 feet per minute (8 miles per hour).

Experience with bait traps has shown that the success of a given trap is strongly dependent on its precise location. Consequently, in analyzing the recoveries of tagged *H. pusio*, it is important to consider the capacity of each trap to collect gnats. By comparing the captures of tagged gnats with those of wild gnats not tagged and released, it is possible to show which traps have taken unexpectedly larger or smaller numbers of tagged individuals. The hypothesis being tested is that the tagged gnats are distributed like the wild ones. It is assumed that both will be caught in the same proportions. On this basis, for any trap an expected number of tagged *H. pusio* is obtained by multiplying the total number of tagged *H. pusio* by the ratio of the number of wild *H. pusio* in the given trap to the total number of wild *H. pusio*. In effect, the tagged *H. pusio* are merely apportioned to each trap on the basis of the occurrence of the untagged or wild individuals. The numbers observed and

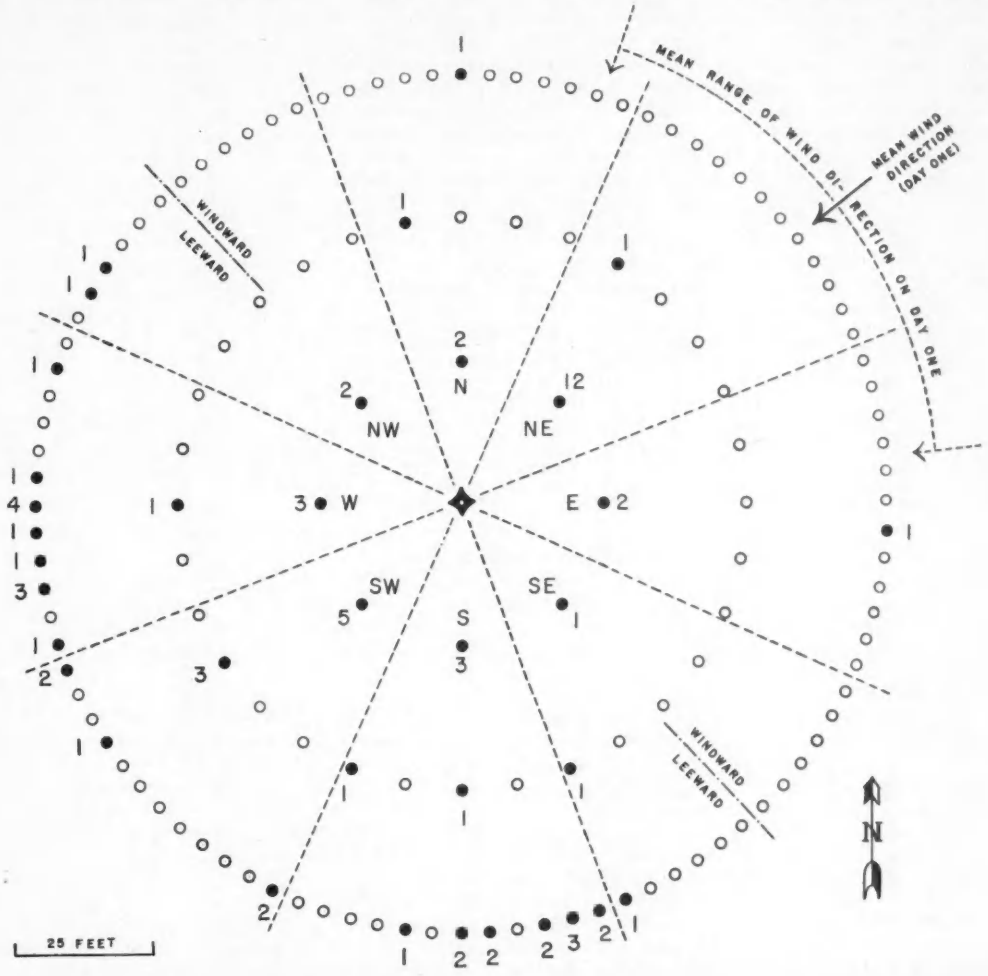

FIG. 2.—Recovery of tagged *H. pusio* at short distances from the release point, Thomasville, Georgia, August 1952. Each small circle or dot represents one of the baited traps arranged in three concentric circles around the release point. The solid dots represent traps which caught tagged *H. pusio* on day 1, the numeral beside the symbol showing the number of radioactive specimens. The radiating dotted lines separate the sectors used in the analysis.

expected can be compared directly, and, if the collections are sufficiently large, as they were in later tests, it is possible to evaluate (by means of chi-square) the probability of any consistent disproportion in the catches of tagged and untagged gnats.

When applied to the short-range recovery test, this method substantiates the interpretation of the results which was based on the tagged gnats alone. Though the collections made on day 2 were never identified, those made on day 3, when the wind had nearly subsided, are believed to represent as fairly as possible the ability of each trap *as sited* to collect wild specimens of *H. pusio*. When the total number of untagged *H. pusio* taken in the outermost circle of traps on day 1 is apportioned to each sector on the basis of the catches on day 3 (table 3, column 3), it is seen that the untagged specimens in four sectors are fewer than would be expected on the basis of the collections made on day 3, and that the disproportion is more obvious in the 3 sectors located upwind (N, NE, E). In other words, on day 1, with a stronger wind than on day 3, relatively fewer untagged gnats were caught on the windward side of the outermost circle.

When the tagged *H. pusio* taken in the outermost circle of traps on day 1 are apportioned to each sector on the basis of the untagged specimens (table 3, column 5), it is apparent that the tagged specimens were most unlikely to be trapped upwind. The disproportion of tagged *H. pusio* taken upwind and down (2:32) is marked (chi-square is 7.4) even when considered in terms of the untagged specimens (133:325). On the other hand, the proportion of tagged *H. pusio* caught in the NW and SE semicircles (18:16) is not different (chi-square is 0.003) from the corresponding proportion of untagged specimens (252:206). This finding gives additional proof of the strong orientation of the trap catches with respect to the wind direction.

A further point should be made in relation to the small number of tagged *H. pusio* that was trapped directly downwind in the SW sector of the outermost circle. Possibly the gnats were more likely to move at an angle to the wind direction (so that more would be trapped in the south and west sectors), but the smaller expected number of gnats in the SW sector suggests that the traps in that arc were less efficient. Another possible explanation is that the sectors with the largest numbers of trapped gnats were in areas where, because of the wind direction, the accumulation of the bait odor from different traps was the most concentrated.

Fortunately, for the type of statistical analysis presented, completely normal distributions are not required. On the other hand, it is of much interest that the distributions of the numbers of both tagged and untagged *H. pusio* in the outermost circle of traps on day 1 were found to approximate closely the theoretical frequencies of the negative binomial. In the tests for goodness of fit, the values of P were 0.52 for the tagged *H. pusio* and 0.43 for the untagged specimens.

Table 3.—Comparisons of observed and expected numbers of *H. pusio* taken in outermost circle of traps of the short-range recovery test: untagged specimens of first vs. third day, and tagged vs. untagged specimens of first day.

Sector	Obs. no. not tagged day 3	Exp. no. not tagged day 1	Obs. no. not tagged day 1	Exp. no. tagged day 1	Obs. no. tagged day 1
NE	109	49	24[a]	1.7	0[a]
E	53	24	15[a]	1.1	1[a]
SE	57	26	46	3.4	1[a]
S	192	86	111	8.2	12
SW	136	61	54[a]	4.0	5
W	145	65	99	7.3	12
NW	124	56	62	4.6	2[a]
N	201	91	47[a]	3.5	1[a]
	1017	458	458	33.8	34

[a]Observed number less than expected number.

HALF-MILE RELEASE TEST

Procedure.—After completion of the preliminary studies, a full-scale release test was undertaken about 15 miles east of Thomasville, Georgia, in the small town of Barwick. This community of approximately 500 persons occupies a residential area of irregular shape which covers about ⅓ square mile. There are chicken yards and stables in all sections, and the whole town is distinctly rural in character. For the purpose of this study, the intersection of the railroad and the main street was selected as the geographical center.

The prevailing summer winds in the vicinity of Barwick are southwesterly, and the location chosen for the release point was windward of the town, ½ mile SW from the geographical center.

The release box was placed on the ground in a depression in the middle of a small cornfield which had many of the stalks still standing. The site was partly surrounded by bushes and trees. Sixteen traps set in a circle, each 50 feet from the release point, were operated on the day of release only.

Forty-seven other traps, mostly in or near the residential section of Barwick, were operated for 5 days starting on the day of release. The traps were set at locations of two types: near enclosures for poultry and domestic animals, where *H. pusio* can be caught in large numbers, and distant from such attractants, where the captures of *H. pusio* are usually smaller (Dow and Hutson 1958). All collections were made in the latter part of the afternoon, at which time, on days 1 to 4, the jars for the next collection were put in place, and the bait also was changed.

A very large number of *Hippelates*, perhaps 50,000, was collected in liver-baited traps on August 30, 1952, transferred to the release box, and fed on a solution of honey and water containing approximately 275 microcuries of P^{32} per milliliter on August 31. On the morning of September 1 (day 1), after all the traps had been set, the release box was opened at the chosen site about 11 a.m. During the day the wind velocity near the release point ranged from less than ½ to more than 7 miles per hour; the mean of 7 observations was about 3 m.p.h. The wind direction, as observed at various times and in different parts of Barwick on day 1, ranged from ESE through S to WNW. The prevailing direction appeared to be SSE.

Results.—On day 1, the circle of 16 traps surrounding the release point caught a total of 1,149 untagged specimens of *H. pusio* and only 12 tagged specimens of this species (table 4). When the collections of untagged specimens were used to calculate for each site an expected number of tagged *H. pusio*, the observed number was found to be greater than the expected number in 6 traps, 4 of which had been upwind from the release point at different times during the release period. The capture of an excess of specimens upwind rather than downwind, as in the short-range recovery test, is believed to be related to the lower wind velocities observed.

In the course of 5 days, the remaining traps

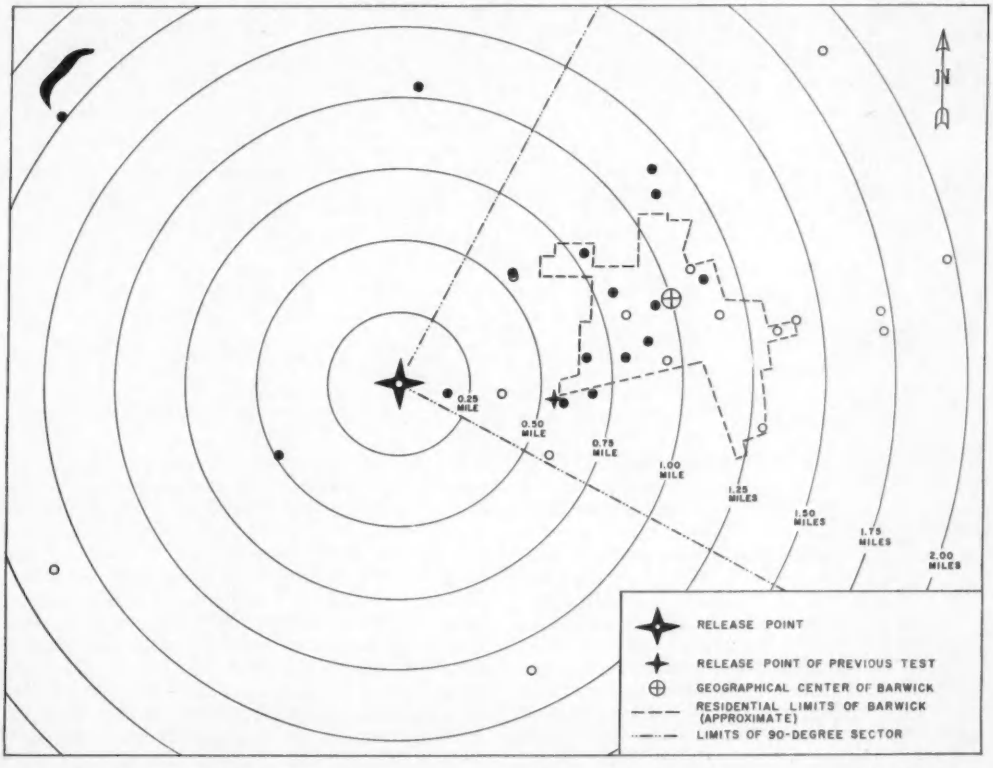

FIG. 3.—Recovery of tagged *H. pusio* released 1 mile from the geographical center of Barwick, Georgia, September 1952. Each small dot or circle represents a baited trap. The solid dots represent traps which caught tagged *H. pusio* within 4½ hours after the start of the release. The concentric circles show distances from the release point.

collected a total of 389 tagged *H. pusio* (table 5). The released population of *H. pusio* appeared to have spread over most of the town on day 1 and to have remained uniformly distributed for the duration of the test. No tagged *H. pusio* were recovered in any of the 5 traps located more than half a mile from the release point toward the south, west, or north.

Discussion.—Considerable difficulty was met in sorting the tagged specimens from the untagged remainder of the trap collections. Much of the trouble was probably due to the spread of radioactive material excreted and perhaps also regurgitated by tagged individuals. Without doubt the situation was aggravated by the moisture remote possibility that some of the recovered gnats were hitchhikers.

ONE-MILE RELEASE TEST

Procedure.—When the results of the half-mile release test were apparent, it became advisable to determine whether *H. pusio* released 1 mile from the middle of Barwick would make a similar invasion of the town. The location chosen for the release point was in a large level pasture WSW (W 17° S) of the geographical center. Eight traps were set in the eight principal compass directions 50 feet from the release point. There were 34 additional traps within a radius of 2 miles (figure 3), also seven traps from 3 to 7

Table 4.—Recovery of tagged *H. pusio* 50 feet from the release points of the ½-mile and 1-mile release tests.

Compass direction[a]	½-mile release test			1-mile release test		
	Wind direction[b]	No. of tagged *H. pusio*[c]		Wind direction[b]	No. of tagged *H. pusio*[d]	
		Expected	Observed		Expected	Observed
NNE		0.64	1*			
NE		1.25	1		18.6	15
ENE		1.22	1			
E		0.49	0		7.3	5
ESE		0.84	0			
SE		0.66	1*		16.6	28*
SSE	4	1.42	2*			
S		0.66	1*	2	5.8	15*
SSW	1	0.18	0			
SW		0.50	0	2	6.4	9*
WSW		0.73	0			
W	2	0.77	3*		6.3	1
WNW		0.21	0			
NW		0.89	0		9.8	5
NNW		0.94	0			
N		0.61	2*		16.1	9
		12.01	12		86.9	87

*Observed number greater than expected number.
[a]Of wind observations (columns 2 and 5), and of trap locations with respect to release point.
[b]Times observed near release point at compass direction indicated.
[c]Recovered on day 1 in traps located in indicated direction from release point.
[d]Recovered on day 1 (3-hour collection) in traps located in indicated direction from release point.

which condenses in jars containing large numbers of gnats. To exclude specimens marked only by contamination, the minimum permissible level was set at 500 c.p.m. as of the day of capture. In some cases, tagged individuals probably survived beyond the date of capture and continued to lose radioactivity faster than the rate of natural decay. This situation would not affect the inclusion of more than a few specimens, however.

Because the personnel conducting the test had driven vehicles directly from the release point to various parts of Barwick on day 1, the very rapid penetration of the town by *H. pusio* appeared to be subject to some question. The following test, however, confirmed the results of the half-mile release so completely that there remains only a miles distant from which no collections were made until the third and fourth day.

A very large number of *Hippelates*, perhaps 40,000, was collected on September 16, 1952, and fed in the release box in the laboratory from about 6 p.m. that evening. The tagging solution of honey and water contained approximately 125 microcuries of P^{32} per milliliter on that date. The following morning (day 1), after the traps were set, the release box was put in place and opened at 10:33 a.m. Thirty minutes later, more than half of the gnats seemed to have escaped; walking around the release box stirred up the remaining specimens and appeared to cause more to leave. An hour after the box was opened, the windows were covered with cardboard, and a

fitted paper cover was lowered over the top. Then and just before the box was closed at 12:13 p.m., the box was beaten and turned about. When closed, the box contained an estimated 100 live gnats.

Because of the very rapid dispersal of *H. pusio* in the previous test, two collections were made in this test on day 1: the first 3 to 4¼ hours after the beginning of the release period, and the second, 6 to 7½ hours after the beginning of the release period. Various precautions were taken to avoid the unintentional transportation of tagged gnats. The truck used to pick up the collections was not the one used when the traps were baited, a residual insecticide had been sprayed inside the truck's cab, the collecting was begun on the further side of the town, and the starting place was approached by a long, circuitous route. Another safety measure was to leave the bait in each trap unchanged throughout the test.

The traps in the circle surrounding the release point were operated for the first period only. As in the previous test, the jars for day 2 and day 3 were put in place the previous afternoon. No collections were made after day 3 except from the seven traps more than 3 miles from the release point. These were set first on the afternoon of day 2 and operated for 2 days only.

On day 1, the wind direction, observed near the release point while the traps in the circle were in operation, ranged from SSE to SW. Measurements of the wind velocity ranged from 4.5 to 12.5 miles per hour. There was an estimated mean of 7 m.p.h. at the times of observation.

Results.—Eighty-seven tagged specimens of *H. pusio* were recovered in the eight traps 50 feet from the release point (table 4). When these collections were analyzed in terms of the 2,313 (partly estimated) untagged *H. pusio* taken from the same traps, the observed number of tagged gnats was found to be greater than the expected number in three traps located upwind (to the SE, S, and SW). The fact that the SE trap was somewhat downwind from the observed directions

Table 5.—Totals, by trapping period and distance from release point, of tagged *H. pusio* recovered in the ½-mile and 1-mile release tests at all distances greater than 50 feet and less than 2 miles.

Miles from release point	One-half-mile release test						1-mile release test				
	No. of traps	Recoveries of tagged *H. pusio*					No. of traps	Recoveries of tagged *H. pusio*			
		Day 1	Day 2	Day 3	Day 4	Day 5		Day 1, 3-hour coll'n	Day 1, 6-hour coll'n	Day 2	Day 3
0.01–0.25	6	88	9	2	6	3	1	20	46	37	11
0.25–0.50	14	104	29	10	17	11	2	2	4	5	9
0.50–0.75	14	34	18	13	19	5	6	11	37	29	5
0.75–1.00	6	4	2	2	4	4	7	15	35	38	12
1.00–1.25	3	1	1	1	2	0	9	15	27	56	15
1.25–1.50	1	0	0	0	0	0	4	0	10	9	2
1.50–1.75	1	0	0	0	0	0	3	1	5	16	2
1.75–2.00	2	0	0	0	0	0	2	0	0	7	0
	47	231	59	28	48	23	34	64	164	197	56

Table 6.—Analysis, based on the weight of the nonradioactive gnats in each trap collection, of the recoveries of tagged *H. pusio* in a 90-degree sector of the 1-mile release test.

Miles from release point	No. of traps	Observed vs. expected numbers, respectively, of tagged *H. pusio*			
		Day 1, 3-hour collection	Day 1, 6-hour collection	Day 2 collection	Day 3 collection
0.01–0.75	8	31>15	83>49	69>61	18>12
0.75–1.00	7	15>10	35>29	38>34	12=12
1.00–1.25	7	7<11	19<28	42>34	11=11
1.25–2.00	7	0<16	11<42	25<45	3< 8
		χ^2=37.2	χ^2=41.2	χ^2=12.1	χ^2=6.17
		P<.001	P<.001	P<.01	P>.10

*To simplify table, expected numbers have been rounded to integers.

of the wind may possibly be related to the greater wind velocity on day 1 of this second full-scale test. In other words, the stronger wind may have swept some of the gnats toward the east.

In the course of 3 days, the remaining traps caught a total of 481 tagged *H. pusio* (table 5). (No tagged *H. pusio* were found in any of the traps more than 3 miles from the release point.) The released population of *H. pusio* appeared to have spread well into the town within 4 hours after the opening of the release box (figure 3 shows which trap sites were positive in the 3-hour collection). In fact, only seven more trap sites became positive in the 6-hour collection and only five more on days 2 and 3. Fifteen tagged *H. pusio* were collected over 1 mile from the release point less than 3½ hours after the opening of the release box.

Discussion.—To evaluate the recoveries of the 1-mile release test on a more quantitative basis, it was desirable to know if the tagged gnats showed any signs of increased mortality or unusual behavior. This was investigated by comparing the tagged and untagged collections of the 34 principal traps. The untagged gnats of each separate catch were dried in an incubator and weighed. It was not considered necessary to estimate and subtract the numbers of *H. bishoppi* because this species is greatly reduced by mid-September (Dow and Hutson 1958).

During the 3 days of the test, the recoveries of tagged *H. pusio* in the 34 principal traps dropped from 228 to 197 and then to 56. There was a similar decrease, however, in the untagged gnats, whose numbers, estimated from their weight, dropped from 192,000 to 180,000 and then to 62,000. Consequently the decrease in tagged *H. pusio*, on a percentage basis, was from 0.12 to 0.11 and finally 0.09. This dimunution appears inconsequential when it is recalled that the tagged population, unlike the wild one, could not receive any replacements.

In the 136 trap catches of the 34 principal traps, there was highly significant correlation (0.57) between the number of tagged *H. pusio* and the weight of the untagged gnats. Relatively fewer tagged specimens were recovered between 1.25 and 2.00 miles from the release point, but the correlation even in this zone by itself was significant (0.49). There were also relatively fewer tagged specimens in the traps distant from animal enclosures, but no evidence was found to prove that this was due to a difference between tagged and untagged gnats. In fact, except for their distribution in time and space, there seemed to be no difference between the two populations.

The 1-mile release test was analyzed in terms of the potentialities of each trap by calculating expected numbers of tagged *H. pusio* for each catch of every trap in the 90-degree sector located ENE of the release point. The limits of this sector, which included the whole town of Barwick, were the radii 45 degrees each side of the radius which passed through the geographical center (figure 3). The expected number of tagged *H. pusio* for a particular trap in a given collection (3-hour, 6-hour, day 2, or day 3) was obtained by multiplying the total of tagged *H. pusio* taken in the given collection by the ratio, in weight, of the untagged gnats in the particular trap to all the untagged gnats in the given collection. The expected and observed numbers of tagged *H. pusio* were then grouped by the distance of the traps from the release point, and the value of chi-square was calculated for each collection (table 6).

The assumption underlying this analysis is that when the released specimens have dispersed throughout the sector, they will be in equilibrium with the unmarked wild population. The progressive decrease of the value of chi-square on days 1 to 3 is believed to indicate the gradual attainment of this uniformity. By using observed and expected numbers to analyze the spread of the tagged gnats, it was possible to ignore any differences in the success of individual traps.

When this *trap-potential* method of analysis was subsequently applied to the ½-mile release test, it was no longer possible to obtain counts or weights of the untagged specimens. The only suitable data were the weights of the untagged specimens of the 4 collections in the 1-mile release test, and these, unfortunately, were available for only 23 of the traps within the 90-degree sector bisected by the line from the ½-mile release point to the geographical center of Barwick. Nevertheless, the values of chi-square for the 5 days of the half-mile release test showed an overall decrease just as in the 1-mile release test (118, 13.2, 8.04, 8.14, and 0.93, respectively, each with 3 degrees of freedom). It is believed that this method of analysis can be applied successfully to a wide range of dispersal studies, and is especially suitable if the trap or place of capture has a variable potential as a source of the organism under study.

The behavior of the four traps located in the outskirts of Barwick to the east and northeast deserves special comment. These traps took a total of 5 radioactive *H. pusio* in the ½-mile release test and a total of 19 radioactive *H. pusio* in the 1-mile release test. The expected totals of *H. pusio* in these traps were 50 in the first test and 67 in the second. The great discrepancy between observed and expected numbers suggests that there was a tendency for the released gnats that reached Barwick to remain there. If this is true, and if *H. pusio* is likely to congregate in suitable habitats, there is hope of finding some economical method to control the adults. Otherwise the results of these flight behavior tests indicate only that soil treatment of an area 2

miles in diameter will not protect any part of it from invasion by adult gnats.

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THE INSECT EPICUTICLE AND ITS TERMINOLOGY[1]

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ABSTRACT

An historical account of the principal discoveries which have led to modern concepts of epicuticular structure is given, and an epicuticular terminology based on present knowledge is proposed.

HISTORICAL

One of the first to recognize that a thin superficial layer of the insect cuticle differed in composition from the remainder was Odier (1823), who extracted from the elytra of cockchafers a brown "oil" which he observed to be deposited on the surface of hardened parts of the cuticle soon after the beetle emerged from the pupa. From his account it is clear that he investigated part of what is now called the epicuticle. Little more was known of its composition until Kühnelt (1928) demonstrated that it was a thin non-chitinous membrane impregnated with fatty acids and cholesterol. He drew an analogy between it and the cuticle of plants.

Kühnelt's findings were confirmed and amplified by Wigglesworth (1933) in his first paper on *Rhodnius* in which he claimed that "the epicuticular substance is not a protein, carbohydrate, or a simple fat; its properties suggest that it might be a complex fatty or waxy substance or mixture." He summarized his views in the words: "The epicuticle is composed of material for which the name "cuticulin" is proposed, which has chemical properties like those of the cutin or suberin of plants, and is perhaps a complex mixture of fatty or waxy substances." Cuticulin, so defined, was a highly-polymerized, non-proteinaceous, lipoid. His views thus differed from those of Kühnelt only to the extent that what Kühnelt had regarded as one constituent of the epicuticle, was, according to Wigglesworth, its principal component. Wigglesworth's failure to recognize protein in the epicuticle in 1933 can largely be ascribed to general lack of knowledge of its chemical composition at that time.

Two years later, Ramsay (1935) observed that cuticulin formed a thin surface film on the cuticle of *Periplaneta*, while Bergmann (1938) extracted from the exuviae of silkworms a mixture of paraffins which had "chemical properties similar to those described by Wigglesworth for cuticulin."

The true composition of the epicuticle remained unknown until the appearance, in 1940, of two fundamentally important papers by Pryor, on whose work all later epicuticular research has been based. In the first of these papers, Pryor (1940a) proposed "the name 'sclerotin' as a general term to describe proteins . . . which owe their stability to a process of natural tanning." In the second (1940b), he wrote, "although it [the epicuticle] does contain highly polymerized and insoluble lipids of the type of cuticulin . . . it seems reasonable to suppose that it is composed mainly of sclerotin . . . . Evidently, the epicuticle is secreted as a simple protein, and is only

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later "tanned and impregnated with lipids." The importance of these statements can scarcely be overestimated since they clearly expressed, for the first time, the modern concept of a fundamentally-proteinaceous epicuticle. The earlier idea of an epicuticle composed chiefly of cuticulin was henceforth tacitly dropped.

The next advance was made by Richards and Anderson (1942), who first demonstrated the composite structure of the epicuticle by separating that of *Periplaneta* into two chemically distinct layers. Accepting Pryor's hypothesis, they suggested that the epicuticle was originally secreted as a simple protein, subsequently tanned, and then differentiated by lipoid impregnation into a thin outer layer containing lipoid, and a thicker, inner layer without lipoid.

Table 1.—The four 'cuticulins'

Type	Author and Year	Anatomical position	Chemical composition
Cuticulin (I)....	Wigglesworth, 1933	The epicuticle as then known	"a complex mixture of fatty or waxy substances" (non-proteinaceous)
Cuticulin (II)...	Wigglesworth, 1947	That part of the epicuticle internal to the 'polyphenol layer'	"a polymerized lipoprotein subsequently tanned with quinones" (=Pryor's 'sclerotin')
Cuticulin (III)..	Dennell and Malek, 1955	The inner part of the cuticulin (II) layer of sclerites	"protein . . . impregnated . . . with lipoid and a further protein possessing an aromatic group;" (tanned)
Cuticulin (IV)..	Dennell and Malek, 1955	Similar to cuticulin III but confined to arthrodial membranes	"a simple protein having an isolectric point of about pH 2.8" (untanned)

Dennell (1946) showed that the epicuticle of *Sarcophaga* was also two-layered. The outer layer was characterized by its high lipoid content; the inner was "fundamentally a layer of protein." He named these the 'lipoid epicuticle' and 'protein epicuticle', respectively. Richards (1957) has recently shown that the epicuticle of another species of *Sarcophaga* also consists of two layers (referred to by him as the "outer epicuticle" and the "inner epicuticle", respectively); these are clearly recognizable in the series of photographs which illustrate his article.

By the time that Wigglesworth began his reinvestigation of *Rhodnius*, Pryor's influence had permeated all epicuticular research, and it had become obvious that cuticulin formed a minor component only of the epicuticular substance. Accordingly, Wigglesworth (1947) reversed his earlier view, and described the epicuticle of *Rhodnius* as consisting of "polymerized lipoprotein subsequently tanned with quinones." Unfortunately, he applied to this material the name 'cuticulin' without explicitly stating that, in doing so, he was using the word in a sense directly opposed to his former usage. A second 'cuticulin' was thus introduced into the literature. Where it is necessary, in this paper, to distinguish between the two, the original non-proteinaceous 'cuticulin' will be referred to as 'cuticulin' (I); its proteinaceous successor as 'cuticulin' (II).

By demonstrating in the epicuticle, two zones differing in their resistance to chemical attack, he brought *Rhodnius* into line with *Periplaneta* and *Sarcophaga*.

External to the 'cuticulin' (II) layer, he distinguished three additional layers—the 'polyphenol', 'wax', and 'cement' layers, respectively. These call for no comment at this stage except to remark that the 'cuticulin' (I) observed by Ramsay (1935), and that which Bergmann (1938) had extracted, almost certainly represented the material of the wax layers of the species concerned.

Webb (1947) distinguished five layers in the epicuticle of *Eomenacanthus*. The outer four he homologized with the four recognized by Wigglesworth (1947) in *Rhodnius*. The fifth layer was internal to the 'cuticulin' (II) layer. These layers were distinguished by staining only, and no tests for chitin were applied. Since *Eomenacanthus* is the only species in which a sub-cuticulin, epicuticular layer has been distinguished, and since Neuffer (1954) recognized three epicuticular layers only in the Mallophaga which he studied, (including *Eomenacanthus*), the presence of the sub-cuticulin layer *as part of the epicuticle* has yet to be confirmed.

A year later, Wigglesworth (1948) identified in *Tenebrio* four epicuticular layers corresponding to those of *Rhodnius*, and Kramer and Wigglesworth (1950) subsequently interpreted the epicuticle of *Periplaneta* in similar terms.

In the epicuticle of *Diataraxia*, Way (1950) distinguished cuticulin (II), wax and cement layers; the cuticulin layer chemically resembled the lipoid epicuticle of *Sarcophaga*.

As a result of their recent investigation of *Periplaneta*, Dennell and Malek (1955) confirmed the presence of two zones in the cuticulin (II) layer of the epicuticle which they homologized with those of *Sarcophaga*. These they named

the 'cuticulin' and 'paraffin' layers. By thus applying to part of the 'cuticulin' (II) layer, the name which Wigglesworth had used since 1947 for the whole of it, they created 'cuticulin' (III). But they also applied this name to the innermost part of the epicuticle of the arthrodial membranes, though its material was not tanned, gave "no indication of the presence of lipoid", and could "provisionally be regarded as being composed of a simple protein." 'Cuticulin' (IV) thus came into being.

Comparison of the distinguishing characters of the four 'cuticulins' (table 1) shows 'cuticulin' to be chemically meaningless; except in its original sense, it has never been defined, and is now incapable of definition. In senses III and IV it is merely being used as a synonym for "inner"; while the chemical meanings of I and II are directly opposed. In these circumstances, the elimination of 'cuticulin' from the terminology is much to be desired.

In addition to giving to the two zones of the 'cuticulin' (II) layer the status of separate layers, Dennell and Malek refused to recognize the polyphenol layer on the grounds that it could not be distinguished as a discrete structure in the mature epicuticle. While admitting the polyphenols were aggregated during a certain stage of epicuticular development, they claimed that these subsequently impregnated the underlying 'cuticulin' (III) layer thereby terminating their separate existence. They confirmed the presence of both wax and cement layers.

Takahashi (1956) distinguished five layers in the epicuticle of *Bombyx*, which he referred to as 'cuticulin' (III), paraffin, protein, wax, and cement "sub-layers", respectively. The first two corresponded with the two inner layers of *Periplaneta* as interpreted by Dennell and Malek. The outer two were the generally accepted wax and cement layers. Separating these two groups was the "protein sub-layer", rich in tyrosine, and containing dihydroxyphenols. Takahashi homologized it with the polyphenol layer of *Rhodnius*, *Tenebrio*, and *Periplaneta*, but claimed that "the protein constitutes a distinct structural layer formed simultaneously with the penetration and impregnation in the underlying layer." It thus functioned as a polyphenol layer, but its protein constituent persisted structurally in the mature epicuticle.

THE PARTS OF THE EPICUTICLE

From the foregoing interpretations, and others available in the literature, the insect epicuticle apparently varies greatly, both in the number of its component layers, and in their respective chemical compositions.

Despite their use of the electron microsope, Richards and Anderson (1942) recognized a single epicuticular layer only in *Aëdes* larvae. Bipartite epicuticles have been distinguished in *Sarcophaga* (Dennell 1946), *Persectania* (Lower 1957a), *Aphodius* (Lower 1957b), *Pseudococcus* and *Epicoccus* (Lower 1957c), *Agrotis* (Rawat 1957), and *Ctenolepisma* (Lower 1959). Three layers occur in *Diataraxia* (Way 1950), the Mallophaga (Neuffer 1954), and *Smynthurus* (Lower 1959); while *Rhodnius*, *Tenebrio* (Wigglesworth 1947, 1948), *Periplaneta* (Kramer and Wigglesworth 1950, Dennell and Malek 1955), and many species of Hemiptera (Lower, unpublished data), all have quadripartite epicuticles. Finally, there is the five-layered epicuticle of *Bombyx* (Takahashi 1956).

Much of this variation however, is man-made rather than real, and originates from the word "layer" being used in two different senses. Thus the two parts which Wigglesworth (1947) observed in the 'cuticulin' (II) layer are treated as distinct 'cuticulin' (III, IV) and 'paraffin layers' in Dennell's scheme. Again, Wigglesworth recognizes a polyphenol layer since such a layer is temporarily present, whereas Dennell does not, because of its impermanence.

The author believes it would be in the interests of homology and terminology if the word 'layer' were used in a restricted and ontogenetic sense. He suggests that the word be reserved for those parts which persist as distinct structural units in the mature epicuticle, and which can be distinguished at time of formation by virtue of their major chemical components. When such layers are subsequently differentiated, the differentiated parts would be referred to as zones, their names being derived from their chief chemical constituents. An alternative is that any layer which can be distinguished as such in the mature epicuticle, be called a layer, and no valid objection can be raised against this practice. But before a uniform terminology can be devised, one or other of the two alternatives must prevail. At present, some workers use one method, others the second, and still others a combination of both. The author admits that his advocacy of the first alternative contradicts what has hitherto been his practice, but work on moulting insects now in progress, and the confused state of the terminology, have compelled him to make the change.

Application of the proposed modification to some selected examples will serve to illustrate the resulting simplification. The 'cuticulin' (II) and its equivalent, the 'cuticulin' (III or IV) plus paraffin, "layers", are derived from a single, primary, proteinaceous layer deposited as a protoepicuticle before secretion of the procuticle begins (Wigglesworth 1947, Dennell and Malek 1955, Lower 1957a). Subsequently, it is lipoid impregnated and may, or may not, be 'tanned'. The 'cuticulin' and 'paraffin' "layers" of Dennell are therefore parts of the original primary layer. In *Aëdes* larvae the lipoid may either be wanting, or uniformly dispersed, as it is in *Diataraxia* larvae. Neither of these species therefore exhibits

zonation of the primary layer. In *Periplaneta*, *Rhodnius* and *Sarcophaga*, while the whole layer may or may not be impregnated, there is a tendency for the greater proportion of lipoid to be aggregated in its outer part. Thus, in the paraffin zone of *Periplaneta*, Dennell and Malek (1955) estimated the protein content to be as low as 6%. A single primary layer is thus common to *Periplaneta*, *Aëdes*, and *Diataraxia*, that of the first-named being two zoned.

After applying this simplification, however, real differences in epicuticular structure still exist, as for example, between the epicuticle of *Sarcophaga* with its single primary layer (comprising inner and outer zones or sub-layers), and that of *Periplaneta* which, in addition to the two-zoned primary layer, has a wax and a cement layer, thereby being three-layered. This suggests that a clear distinction is not being made between what is fundamental and what is incidental in the epicuticle. Provisionally excluding *Eomenacanthus*, the primary layer is present in every described insect epicuticle, and it alone constitutes the entire epicuticle of many species, e.g., *Sarcophaga*, *Aphodius*, *Ctenolepisma*, etc. Those which include accessory (polyphenol, wax, or cement) layers have these superimposed on the primary layer. Clearly defined characters distinguish this layer from all others.

1. The primary layer is a component of every described insect epicuticle and is frequently its sole component.

2. The primary layer is secreted before any other part of the cuticle during moulting (Wigglesworth 1933, Dennell and Malek 1955, Lower 1957a). Accessory layers are formed either immediately before, or immediately after, moulting, and are therefore the last part of the cuticle to be secreted. Secretion of the procuticle therefore intervenes between the formation of primary and accessory layers if the latter are present.

3. The primary layer is always directly secreted by the hypodermis; accessory layers may be secreted by other agents.

4. Once the primary layer is complete, the secretory activity by which it was formed normally ceases. If abraded, the insect is apparently unable to restore the lost parts (Lower 1957b). Accessory layers, if abraded, are rapidly replaced; their secretion appears to be a continuous process by which they are maintained intact during the life of the instar.

5. The primary layer apparently always undergoes secondary chemical modification by being lipoid impregnated, and frequently tanned. Accessory layers do not change in composition once they have been deposited.

6. The primary layer is practically unaffected by fat solvents. It is relatively resistant to alkalis and acids, and its outer zone is attacked only by hot, violently-oxidizing mixtures which which bring about its chemical disintegration. A strong physico-chemical union binds it to the underlying procuticle. Accessory layers are readily dissolved, or mechanically displaced, from the primary layer.

Considered collectively, these facts indicate fundamental differences between primary and accessory layers. So far as is known, the primary layer is homologous throughout the class, and it appears to be the insect epicuticle in the real sense. It may be defined as the non-chitinous outer part of the cuticle, originally secreted as a proteinaceous layer by the hypodermis before any other part of the cuticle is secreted, its composition being subsequently modified by lipoid impregnation. It may or may not undergo "tanning".

Since this definition excludes all accessory layers, the need arises for a term to include all of these collectively, irrespective of their number and composition. Richards (1951), on histological grounds, suggested substituting "tectocuticle" for "cement layer"; but this does not meet the need for a comprehensive term which will include all accessory layers. Further, the author believes that any term ending in "-cuticle" should be applied only to fundamental parts of the cuticle. As has previously been pointed out (Lower 1956), even the term 'epicuticle', now unfortunately too firmly entrenched to be ejected, is a complete misnomer since it implies the impossible, that a part of the cuticle can be 'upon' the whole of it. For the accessory layers collectively, the term *amphion* (Greek—a garment or cloak) is here proposed.

Table 2.—Comparison of four terminological systems proposed for the outer non-chitinous cuticle of insects

Wigglesworth (1947)	Richards (1951)	Dennell and Malek (1955)	Lower
cement layer wax layer polyphenol layer	tectocuticle lipid epicuticle queried	cement layer wax layer not recognized as a permanent structure	amphion: cement layer / wax layer / polyphenol layer or homologue *if a permanent structure*
outer resistant zone inner less-resistant zone	Cuticulin layer: lipoprotein layer / basal protein layer	paraffin layer cuticulin layer	epicuticle: outer zone / inner zone — if zoned

In species possessing ephermeral polyphenol layers, the amphion comprises wax and cement layers; where the polyphenol layer, or its homologue, persists as a structural part of the mature amphion, the latter is three-layered. An intimate connexion appears to exist between wax and cement layers; one does not seem to occur in the absence of the other. Usually, the cement forms a superficial covering over the wax which it is thought to protect, but Way (1950) has described an interesting condition in *Diataraxia* where the cement layer is net-like and sunk in the wax. It here appears to function as does the steel reinforcing in ferro-concrete.

As to the terms to be applied to parts of the epicuticle, these should be as broad as possible since the data are so few. The use of 'epicuticle' as proposed in this paper enables the mutative 'cuticulin' to be discarded. The expressions, "protein" and "lipoid layers" as used by Dennell are satisfactory, but are liable to be taken too literally by others. It may be that 'epicuticle' in *Diataraxia* and *Aëdes*, or "inner" and "outer zones" of the epicuticle in *Sarcophaga* and *Periplaneta* may serve until adequate knowledge of composition in the future shall make an exact chemical terminology possible. It is most undesirable, at this stage, that any term should be applied to any non-chitinous part of the cuticle which implies that its definitive composition is known. The terminological system here proposed is compared with several others in table 2.

The author's interpretation of the data, and the terminology based on it, must necessarily be tentative, since expanding knowledge may prove it wrong at any time. Of the million or so described insect species, the cuticles of less than one in ten thousand have been even partially studied, and there is not a single species of which our knowledge is adequate. The cuticles of some species not yet examined may possess non-chitinous parts differing fundamentally from those at present known.

In the author's opinion, the principal merit of the proposed terminology is that it is not a terminology. Rather is it a descriptive system which accords with the known facts, emphasizes similarities rather than differences, and by the use of descriptive expressions, leaves the way open for future workers to devise a scientific terminology when the necessary knowledge on which to base it is available. This is the reason why the terms "wax" and "cement" have been retained. Both are handy, innocuous, mnemonics which commit us to no theories concerning their composition. The one new term, 'amphion' draws attention to what the writer regards as a fact of fundamental importance in the interpretation of the structure of the non-chitinous part of the cuticle.

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CHARACTERISTICS OF BLOOD TOXINS IN DDT-POISONED COCKROACHES[1]

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ABSTRACT

The blood of DDT-poisoned cockroaches has been known to contain a neurotoxin which is independent of the DDT content of the blood. This toxin was found to increase in quantity as symptoms of poisoning progressed. Sufficent was present in early stages to cause marked increases in the spontaneous activity of nerve cords excised from unpoisoned individuals, while in late stages of poisoning the toxin could suppress spontaneous activity completely in such cords. Treatment of the sixth abdominal ganglion with the toxin resulted in multiple discharges in giant fibers when cercal nerves were faradically stimulated, and also caused synaptic block. The toxin was found to be dialyzable, and though unstable in whole blood, it was stable in the dialysate.

Sternburg and Kearns (1952) demonstrated the presence of a toxic principle, or principles, in the blood of DDT-poisoned American cockroaches, which was independent of the DDT content of the blood. This toxin could be detected by its effect on the spontaneous activity of the excised ventral nerve cords of cockroaches, when cords were suitably connected to the proper electronic components for observation of spontaneous activity. The toxin caused the appearance of recurrent trains of impulses, or at times caused the abolishment of all activity, or the successive occurrence of both effects.

The presence of the toxic principle in the blood was correlated with symptoms of poisoning; cockroaches showing no DDT symptoms yielded non-toxic blood, while those showing even early symptoms of poisoning yielded toxic blood.

The present investigation was directed toward characterizing the toxin, with regard to some of its physical and neurotoxicological properties, as a forerunner to work on its identification.

MATERIALS AND METHODS

The insects used were adult *Periplaneta americana* (L.). Females were used as sources of toxic and normal blood, and the nerve cords of males were used in the assays of blood samples for toxic activity.

Circuit elements and their connections.—For observations, excised nerve cords were placed in a small lucite electrode box, which was surrounded on all sides by a water jacket, through which water could be circulated. Water from a controlled-temperature reservoir, which could be held at any temperature from 0° to 50° C., was circulated through the jacket, and the temperature of the cord and circumambiant air could thus be held at any desired temperature, or changed during an observation from one temperature to another. Cords were laid in a trough, inside the box, which sloped toward and terminated at a drain hole which went through the bottom of the box.

Across the bottom of the trough were two pairs of platinum stimulating electrodes and two pairs of recording electrodes. The stimulating electrodes were so situated that one pair lay between the fifth and sixth abdominal ganglia, the other near the distal end of the cercal nerve. In experiments where the latter pair was used, the cerci were dissected out with the nerve cord so that the final preparation consisted of the ventral nerve cord from just anterior to the first thoracic ganglion, through the sixth abdominal ganglion, with the cercal nerves and cerci attached. One pair of recording electrodes lay at the base of a cercal nerve, and the other pair between the first and second abdominal ganglia.

Leads from all electrodes were connected to a switch panel so that any combination of stimulating and recording electrodes could be used merely by setting the appropriate switches.

Once the cord was situated in the trough with the electrodes in their proper places, it did not have to be moved for purposes of perfusing or treating with physiological saline solution, toxic blood or other substances.

The recording electrodes were connected to a Grass Instrument Co. Model P 4 preamplifier, the output of which was fed into the Y-input of a Dumont type 304 H cathode ray oscillograph, and also into the bridge-in connection of a Magnecord model PT6J amplifier, and thence to a Magnecord model PT6A tape recorder.

The speaker output of the Magnecord amplifier was fed through a wave-converting discriminator to a Knight 6-watt amplifier (Allied Radio Corp.), and finally to the Geiger-Mueller input of a Scientific Instrument Development Laboratory model 163 scaling unit. These last three elements composed a counting circuit which was used to quantitate nervous activity, using impulses per unit time as an index of levels of activity.

The design of the discriminator[3] was that it could be adjusted to screen out all impulses below

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[3]The discriminator was designed, after a consideration of the requirements of the problem, by Mr. Howard C. Roberts of the University of Illinois Engineering Experiment Station.

any desired level, allowing only those larger than this level to pass through the discriminator to the amplifier and scaling unit. At the same time, it served to convert the diphasic nerve impulses to monophasic pulses more suitable to the circuitry of the scaler.

A Grass Instrument Company model C4B Kymograph camera was used to photograph oscillograph traces. For photographs of various selected levels of spontaneous activity, tape records were first made of the activity, and these, in turn, played back into the oscilloscope. Photographs could then be made of selected portions of these "play-backs".

The stimulating electrodes were connected to the output of a Grass Model S4A stimulator. The camera, stimulator, and oscillograph were connected together so that, for single frame pictures of nerve cord responses to faradic stimuli, the stimulus and the sweep of the oscillograph beam were triggered by, and synchronized with the shutter of the camera. (Details of this hookup are in the manufacturers manual for the kymograph camera).

Samples of toxic blood.—After being anesthetized with carbon dioxide, the cockroaches were treated with a solution of DDT in acetone, usually 125 to 150 micrograms of DDT in 1 or 2 microliters of acetone, applied to the membranous area between and around the prothoracic coxae. They were then placed in battery jars and held for 24 to 48 hours in a humidified cabinet which was thermostatically regulated to 35° C. At the end of 24 hours the insects might or might not be manifesting symptoms of DDT poisoning, but by the end of 48 hours, most of them were at least hyperexcitable. They were then transferred to a 15° C. temperature cabinet, and allowed to remain there until all were prostrate, after which they were bled, one at a time, in the manner described by Sternburg and Kearns (1952), the blood being frozen as soon as it was expressed from the cut ends of antennae or legs. The blood so collected was centrifuged to free it of fragmented hemocytes, and the supernatant frozen and stored in a deep freeze unit.

Method of assay.—Excised cords were placed in a shallow dish containing physiological saline solution, and allowed to remain there for 15 to 20 minutes before being used in assays of experiments. The physiological saline was of the following composition: NaCl, 6.7g.; $CaCl_2$, 0.12g.; KCl, 0.15g.; $NaHCO_3$, 0.15g.; in 1 liter of distilled water (Davenport 1949).

After cords had been arranged on the electrodes, they were left for 5 to 10 minutes before any observations were made of their activity. Cords showing abnormally high activity were discarded.

The normal spontaneous activity of the cord was tape recorded over a period of 5 minutes. The physiological saline in which the cord was bathed was drawn off, and replaced with 50 microliters of the sample to be assayed, which amount was found to be sufficient to cover all parts of the cord. Immediately after this treatment had been made, the tape recorder was started and allowed to run continuously throughout the assay. All routine assays were run at 28° C. If obviously abnormal activity were not forthcoming within 30 minutes, the assay was generally terminated.

To quantitate the activity, the finished tapes were replayed, and by means of the counting circuit described earlier, the numbers of nerve impulses per unit time, at regular intervals, determined. For an evaluation of the normal spontaneous activity, impulses were counted during the first 4 minutes of the 5 minutes it was recorded, these values then being converted to impulses per second. After treatment of the cord with blood, dialysate of blood, or other substances, counts were made over 1 minute periods, the first three being during the first, second, and third minutes after treatment, and the fourth during the sixth minute. Subsequent counts began at each 5-minute interval thereafter.

In all tables, spontaneous activity is expressed in terms of the numbers of nerve impulses of 50 microvolts and larger per second. Frequencies of less than 1 impulse per second are noted as 0-1. Higher frequencies are given to the nearest whole number.

RESULTS AND DISCUSSION

As an aid to the interpretation of the quantitative measures of spontaneous activity, pictorial records of various levels of activity, with their corresponding impulse frequencies are presented in figure 1. In all cases, the discriminator was adjusted to transmit impulses of 50 microvolts and higher. The film speed used in making these photographs was 100 millimeters per second.

This method of quantitating spontaneous activity is not an entirely defining one. The appearance of trains of impulses, such as those in figure 1c, but at less frequent intervals, leads to figures lying within the range of those for normal, untreated nerve cords, and yet, such trains are considered to be induced by the blood toxin. Too, under some conditions, particularly above 30° C., obvious increases in activity may appear in the form of long-lasting trains of impulses of very low magnitude. These impulses are on the order of 20 or 30 microvolts and less, and so are not reflected in the figures expressing frequencies of impulses of 50 microvolts and larger. This disadvantage can be avoided to some extent, of course, by increasing the sensitivity of the discriminator, but an increase of sufficient magnitude to pick up the smallest potentials results in a dangerously narrow margin between the impulses to be counted, and the preamplifier noise and other sources of interference. In fact, some of the trains are composed of spikes of such small poten-

tials that they are all but hidden in the preamplifier noise as it appears on the oscillograph trace, their presence being indicated by a faint, high-pitched note on the audio unit.

Normal spontaneous activity.—Cords excised and prepared in the manner described under Materials and Methods show a range of activity from very low to extremely high. The latter occur only occasionally. Generally, normal activity appears as in figure 1a. Cords may go for 30 minutes or more producing only an occasional impulse of 50 microvolts or larger. In some cases, the activity may increase for a short period of 15 seconds to a minute or so, and then return to the previous level. Among nine cords observed, each over a period of 30 minutes, all had average impulse frequencies of less than one 50-microvolt impulse, or larger, per second. The highest frequency attained in any cord was an average of four impulses per second during a 1-minute period, which was the twentieth minute after the beginning of the observation. These observations were made at 25° C., but similar observations at 15° and 35° showed essentially the same picture.

Toxin concentration in the blood with respect to symptoms of poisoning.—For the purposes of this investigation, three stages of DDT poisoning were considered: 1, hyperexcitable stage, in which the cockroaches, although hyperexcitable, were still capable of coordinated movement; 2, uncoordinated stage, which was characterized by lack of coordination, and occasional tremors or convulsive movements; and 3, prostrate stage, in which the insect was no longer capable of remaining upright. From the beginning of this last stage, time of prostration, rather than symptoms, was the primary criterion used in selecting cockroaches for bleeding.

The cockroaches were treated with 125 micrograms of DDT in 2 microliters of acetone, held for 24 hours at 35° C., and then transferred to 15° C. Fifty cockroaches were selected and bled at the proper times after this transfer to represent each of the first two stages of poisoning. Fifty cockroaches were also used as sources of blood representing each of the three periods considered during the third stage of poisoning. These were one-half hour after becoming prostrate, at which time the legs of the insects were still moving actively, and tremors involving the legs and antennae and muscles of the body wall occurred intermittently; 2 hours after becoming prostrate, at which time most of the activity consisted of slow flexion and extension of the legs, with frequent tremors; and finally, after 5 hours of prostration when the insects were almost completely inactive, except for occasional twitches of legs, antennae, and cerci. Each of the samples collected was centrifuged, and the supernatants used in the assays for toxic activity.

The nerve cord responses to the undiluted supernatants of the blood samples are presented in table 1. Each series of figures represents the average from observations on five cords. The nerve-cord responses to treatment with blood obtained from cockroaches in the hyperexcitable and uncoordinated stages are approximately the same, in that the spontaneous activity of the treated cords increased within 5 minutes after treatment, but did not attain very high levels during the 21 minutes they were observed.

Cord responses to blood obtained from cockroaches which had been prostrate one-half hour, on the other hand, were much more striking. The spontaneous activity increased markedly during the first minute after treatment, and attained very high levels of almost 100 impulses per second during the 21 minutes they were observed.

Blood obtained from cockroaches which had been prostrate for 2 hours showed considerably less toxic activity than that obtained from those which had been prostrate for ½-hour, and was about equal in effect to the blood obtained from hyperexcitable ones. Blood from cockroaches prostrate 5 hours showed a further decrease in toxic activity.

The blood obtained from cockroaches prostrate 5 hours was diluted to 10 percent of its original concentration in physiological saline, and assayed for toxic activity. The responses of cords to this diluted blood are presented in table 2.

The data in table 2 indicate that the diluted sample of blood elicits a much greater response from treated cords than the undiluted sample. Its effects are comparable to those of blood obtained from cockroaches prostrate one-half hour.

Apparently then, the concentration of toxin in the blood of DDT-poisoned cockroaches increases as the stages of poisoning become more advanced. It has a greater effect as the concentration increases to a point, after which it tends to suppress, rather than stimulate spontaneous activity.

Effect of temperature on the activity of toxic blood.—The blood for this experiment was obtained from cockroaches which had been treated with 125 micrograms of DDT in 2 microliters of acetone, held at 35° C. for 48 hours, and then

EXPLANATION OF FIGURE 1

FIG. 1.—Representative levels of spontaneous activity. Only impulses of 50 microvolts and larger were counted in these examples. The film speed used in making these pictures was 100 millimeters per second, and counts were made over 15-second periods. Frequencies are in terms of the numbers of impulses per second. A, less than 1; B, 28; C, 61; D, 67; E, 164; F, 277.

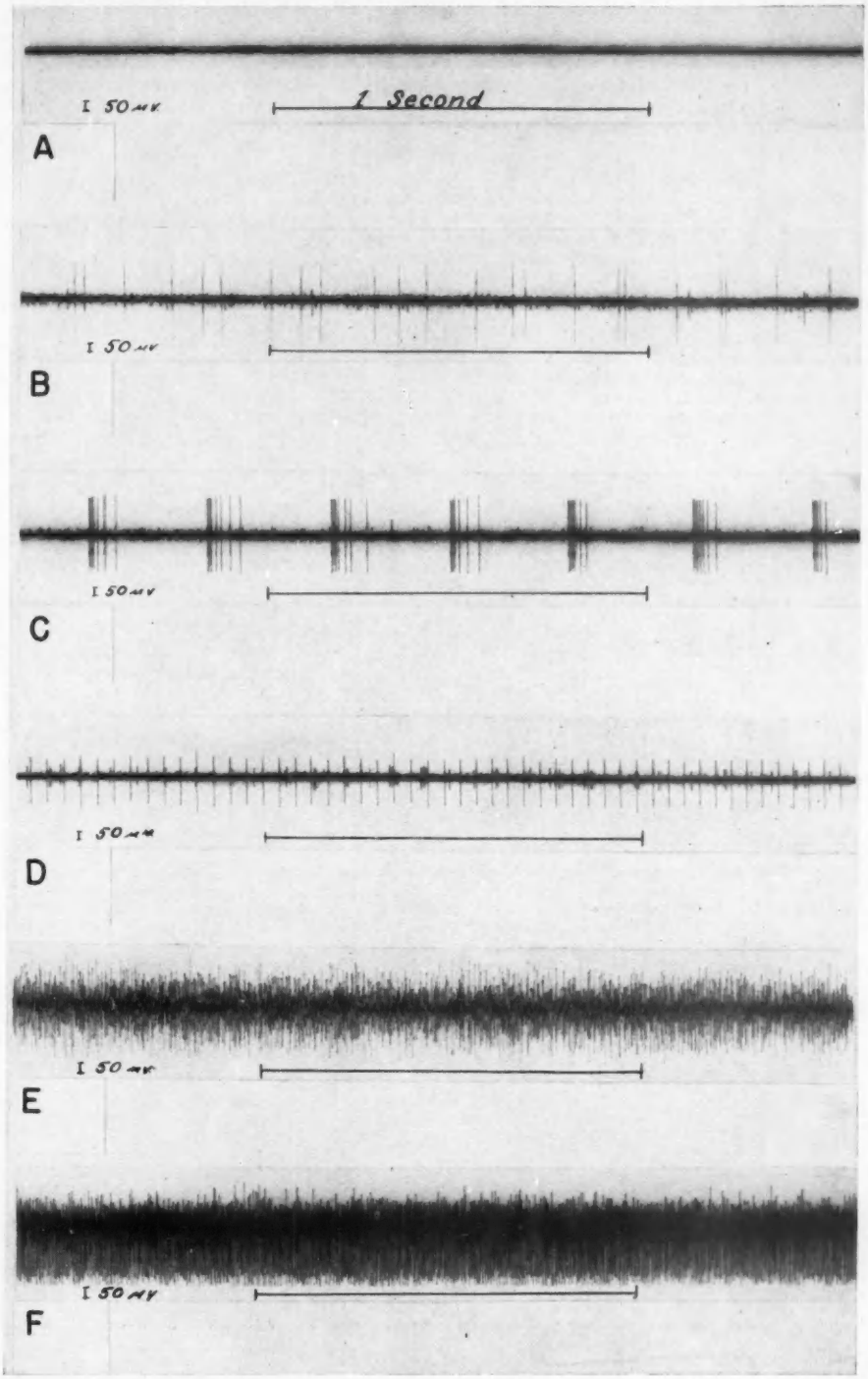

FIGURE 1

transferred to 15° C. until all had been prostrate at least 3 hours. The blood was diluted to 20 percent of its original concentration in physiological saline, and the diluted blood assayed for toxic activity on cords at 34°, 28°, and 15° C. The responses of these cords are shown in table 3.

increased activity, but the highest levels attained at 15° were noticeably lower than the highest at 28°. It has been noted during numerous observations, that the appearance of very-high-frequency trains of impulses, which sound like sirens on the audio unit, are common at 28°, but rarely

Table 1.—Responses of excised nerve cords, in numbers of nerve impulses of 50 microvolts and larger per second, to treatment with the undiluted supernatants of blood obtained from cockroaches in various stages of poisoning. Counts were taken during the 1-minute periods indicated. Each series represents the averages of five cords

Stage of poisoning	Normal level	Minutes after treatment						
		0–1	1–2	2–3	5–6	10–11	15–16	20–21
Hyperexcitable	0.2	8.8	6.4	14.8	13.4	7.8	8.8	12.0
Uncoordinated	0.4	2.0	5.6	1.4	3.2	13.6	20.8	9.4
Prostrate ½ hour	0	27.8	15.8	29.8	37.6	96.2	51.4	61.0
Prostrate 2 hours	1.0	6.0	15.6	17.4	9.0	13.0	1.2	17.4
Prostrate 5 hours	0.6	7.6	3.8	1.4	10.0	12.2	20.8	18.8

Table 2.—Responses of nerve cords to treatment with blood obtained from cockroaches which had been prostrate 5 hours, and diluted to 10 percent in physiological saline solution. Activities are in terms of the numbers of nerve impulses of 50 microvolts and larger per second. Frequencies of less than one impulse per second are noted as 0–1. Higher frequencies are given to the nearest whole number. Counts were taken during the 1-minute periods indicated.

Cord No.	Normal level	Minutes after treatment						
		0–1	1–2	2–3	5–6	10–11	15–16	20–21
1	0–1	16	19	11	36	24	83	72
2	0–1	50	19	16	59	63	88	190
3	3	33	23	8	5	2	56	38
4	0–1	110	90	83	52	91	102	72
5	0–1	11	41	43	44	37	45	48
Average		44.0	38.4	32.2	39.2	43.4	74.8	84.0

Table 3.—Responses of nerve cords at different temperatures to aliquots of the same sample of toxic blood. Each series represents the averages of five cords. Activities are expressed in numbers of nerve impulses of 50 microvolts and larger per second. Counts were made during the 1-minute periods indicated

Temperature °C.	Normal level	Minutes after treatment						
		0–1	1–2	2–3	5–6	10–11	15–16	20–21
34°	0.0	0.0	0.0	0.0	2.6	2.4	4.2	5.4
28°	0.6	12.8	5.2	23.6	58.4	6.0	42.5	67.5
15°	0.8	13.0	22.2	9.0	7.8	8.4	14.4	38.0

The figures for activity at 34° are somewhat misleading, in that all of these cords showed marked increases in low levels of activity which are not reflected in the figures presented. Within 30 seconds after the diluted blood was applied, frequent trains of very small impulses could be heard on the audio unit. In some cases, these trains became prolonged, and lasted as long as 1 or 2 seconds.

At 15° and 28° C., there is marked evidence of

occur at 15°. It should probably be expected that the temperature coefficients of the physicochemical processes involved in the conduction of nerve impulses would be such that there would be a noticeable difference in the upper limits of nerve impulse frequencies at these two temperatures. In such a case, the lessened response at the lower temperature would be a function of the nerve cord and not the toxin.

The reason for the failure of the appearance of

larger spikes at 34° C. is not known. It is known that nerve cords at this temperature are capable of producing large action potentials (giant fiber spikes), at very high frequencies, when mechanically stimulated on the sixth abdominal ganglia.

Effect of temperature on symptoms of poisoning.—To determine the effect of temperature on the symptoms of DDT poisoning, three adult female cockroaches were treated with 150 micrograms of DDT in 2 microliters of acetone, and held for 15 hours at 35° C. They were then, each in turn, transferred to 15° C. until they became prostrate, after which they were returned to the 35° cabinet, where they were impaled through the thoraces, on a copper-constatine thermocouple. As their body temperatures approached that of the cabinet, their symptoms were observed and recorded.

At the beginning of the observations, these cockroaches were very feebly active, showing only slow flexion and extension of their legs, and only occasional tremors, mostly confined to the tarsi and cerci. Between 20° and 23°, tremors becmea more frequent and more violent, involving all of the legs and antennae. None of the insects were capable of making any coordinated movements. Between 25° and 27°, tremors became even more violent, were characterized by spasmodic contraction of the muscles of the body wall and appendages, and occurred at frequent intervals. Still no coordinated movements were seen. Between 28° and 29°, coordinated crawling movements began to appear, but tremors were still occurring. At 30°, tremors ceased to appear, and the cockroaches, when removed from the thermocouple, were capable of running normally.

The transition from a condition in which tremors are apparent and a cockroach is in a hyperexcitable state, to one in which it is apparently entirely normal in its actions, is a fairly fast one, and appeared in these cases at, or very close to, 30° C.

A similar phenomenon can be observed in the spontaneous activity of excised nerve cords. Cords which have been treated with toxic blood, and are exhibiting very high levels of spontaneous activity at 28° C., frequently show a sharp reversal

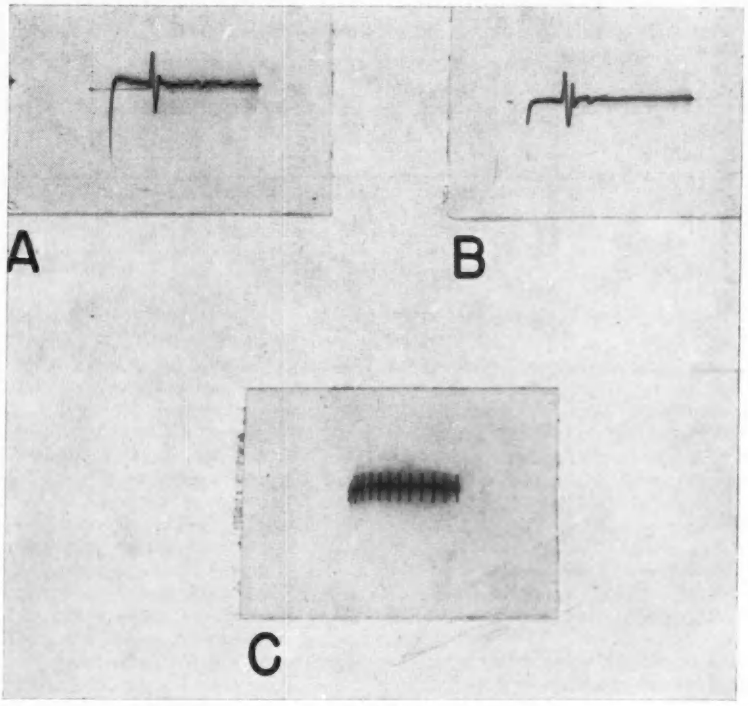

FIGURE 2

FIG. 2.—Responses of excised nerve cords to faradic stimulation. a. Giant fiber response in normal nerve to a single faradic shock to cercal nerve. Recording electrodes were between the first and second abdominal ganglia. b. Giant fiber response to a single faradic shock between the fifth and sixth abdominal ganglia. Recording electrodes as in *a*. c. After discharges in giant fiber in poisoned nerve, as result of single faradic shock to cercal nerve. (Gain reduced). The stimulus artifact is at the left in each trace.

to an apparently normal level as the temperature is brought above 30°.

Since it is possible for DDT-poisoned cockroaches to manifest all of the symptoms of DDT-poisoning at temperatures above 30°, it would not be expected that the above described phenomenon would occur uniformly with all DDT-poisoned cockroaches. It does occur consistently and frequently enough, under the proper conditions, however, to suggest that there is something critical about the temperature at or near 30° C. No explanation of this can be offered at the present time.

Effect of toxin on the response to faradic stimulation.—Normal cords, when stimulated either on the connectives between the abdominal ganglia, or on the cercal nerve, respond to each stimulus with one propagated action potential. Pumphrey and Rawdon-Smith (1937) have shown that after periods of synaptic inactivity, strong cercal stimulation may produce after-discharges in the giant fibers, but this does not occur when the synapses have become adapted through previous activity.

that is, the greater the spontaneous activity of the cord, the lower the threshold.

As mentioned earlier, extremely high levels of spontaneous activity are often followed by blocks, during which there is no detectable activity. During these periods the nerve is apparently completely refractory to cercal stimulation, stimuli as high as 6 volts eliciting no response. Direct stimulation of the giant fibers between the fifth and sixth abdominal ganglia, however, yields a response characteristic of normal, untreated cords, the threshold being within the normal range of 0.15 to 0.20 volts, and the response being one for one to each stimulus.

With the return of spontaneous activity, there was a return of the giant-fiber response to cercal stimulation, in many cases at a higher-than-normal threshold of 1 to 1.5 volts. Response was no longer one for one, but characterized by after-discharges in the form of short trains of impulses, as shown in figure 2c. The response of the giant fibers to direct stimulation however, was still characteristic of a normal cord.

The indications here are that in excised ventral nerve cords the toxin has a site of action on synaptic junctions. Treatment of the sixth abdominal ganglion with blood containing an excitatory level of toxin causes a lowering of the threshold for transynaptic conduction of impulses from the afferent fibers in the cercal nerve to the giant fibers of the ventral nerve cord, without any concurrent alteration of the response of the giant fibers themselves to direct stimulation. Further, failure of the nerve to respond to cercal stimulation during periods when spontaneous activity is blocked, appears to be a function of the synapses, since in this situation too, the giant fibers respond to direct stimulation in an apparently normal manner.

Table 4.—The results of assays of the dialysate of toxic blood, in terms of the numbers of nerve impulses of 50 microvolts and larger per second. Counts were made during the 1-minute periods indicated. Frequencies of less than one impulse per second are noted as 0–1. Higher frequencies are given to the nearest whole number

Cord No.	Normal level	Minutes after treatment						
		0–1	1–2	2–3	5–6	10–11	15–16	20–21
1	3	0–1	0–1	0–1	33	50	64	67
2	0–1	0–1	0–1	5	0–1	63	14	95
3	0–1	0–1	4	13	0–1	85	16	127
4	0–1	0–1	0–1	0–1	0–1	0–1	8	29
5	0–1	4	0–1	3	26	41	39	51

The response of a normal cord to a single stimulus is shown in figure 2a. The response to a single stimulus applied to the connectives between the fifth and sixth abdominal ganglia is shown in figure 2b. In both cases, the recording electrodes were between the first and second abdominal ganglia.

The threshold for single giant fiber response to cercal stimulation, using a square wave of 0.40 milliseconds duration, was found to be normally 0.25 to 0.40 volts, while the threshold for direct stimulation of the giant fibers was 0.15 to 0.20 volts.

Stimulation of the cercal nerve at the rate of one stimulus per second over a period of 1 hour, showed no change in response and no change in threshold. Treatment of the sixth abdominal ganglion with a few microliters of toxic blood, which contained an excitatory level of toxin, caused a decrease in threshold. The decrease amounted to as much as 0.15 volts, and was correlated with the level of spontaneous activity;

Dialyzability of the toxin.—In order to determine whether or not the toxicity of blood can be lost through dialysis, samples of mildly toxic blood were dialyzed against a constantly flowing physiological saline solution. Since, as will be shown later, the toxin in centrifuged blood is unstable, short dialysis periods were to be desired. To

approach this end, blood samples containing only enough toxin to detect by means of the bioassay were used. Such blood was obtained from cockroaches which had been treated with 125 micrograms of DDT in 2 microliters of acetone, held for 24 hours at 35° C., and then transferred to 15°. They were bled as soon as they became prostrate, before use, the supernatant of the centrifuged blood was assayed for toxic activity, and found to be mildly toxic in that it caused the appearance of trains of impulses in 3 to 5 minutes.

Several successive 50-microliter aliquotes of the supernatant were dialyzed for 3 hours against a constantly flowing physiological saline solution, in a microdialysis cell. These dialyses were carried out in a cold room which was held at 3° C. As control, 250 microliters of the supernatant were allowed to stand for 3 hours in a small vial in the cold room.

Assays of the dialyzed blood showed no apparent toxic effects on four of the five cords treated. The fifth cord showed some trains of impulses after 15 minutes.

Assays of the control sample disclosed that it had retained essentially all of its toxicity. The five cords on which it was assayed all showed trains of impulses within 10 minutes, and three of them within 5 minutes.

To determine whether or not the toxic principle could be recovered in the dialysate, blood was obtained from cockroaches which had been treated with 150 micrograms of DDT in 1 microliter of acetone, held at 35° C. for 48 hours, and then transferred to 15° until all had been prostrate for 3 hours. After centrifugation, the toxicity of the supernatant was verified by assaying it on several cords.

Fifty microliters of the supernatant were dialyzed for 3 hours against 250 microliters of physiological saline solution. The results of the assays of the dialysate are presented in table 4.

All of these cords, except No. 4 showed increases in spontaneous activity to levels well above normal in 10 minutes. By the end of 20 minutes, all cords were exhibiting moderately to very high levels of activity.

These two experiments suggest two conclusions. First, that the toxic principle is dialyzable, and second, that the principle does not consist of two or more fractions, one of which is nondialyzable. It is possible, of course, that the principle may consist of two or more dialyzable fractions, but no conclusive evidence for or against this hypothesis is forthcoming from the investigations conducted so far.

Stability of the toxin in blood.—It was known by Sternburg and Kearns (unpublished) that samples of toxic blood, allowed to stand at room temperature for a few hours, lost their toxicity. If this loss were due to the gradual breakdown of the toxin by some means, then, of course, the concentration of the toxin would vary inversely with time. On the basis of what has been found in the present study, it might be hypothesized that samples of blood which have a concentration of toxin which is optimum for eliciting responses from excised nerve cords, would show a decline in toxicity as they were allowed to stand at room temperature, while those having an excess of toxin, that is, a concentration high enough to suppress spontaneous activity, would under like conditions show increases in their effects on excised nerve cords.

Table 5.—Responses of excised nerve cords, in numbers of nerve impulses of 50 microvolts and larger per second, to treatment with the dialysates of toxic blood. Each series represents the averages of five cords

Treatment of dialysate	Normal level	Minutes after treatment								
		0–1	1–2	2–3	5–6	10–11	15–16	20–21	25–26	30–31
Dialyzed only	0.8	2.6	5.6	2.6	20.8	22.0	52.4	48.6	69.4	35.2
Heated to 100° C.	0.6	6.6	1.8	7.8	7.0	15.8	18.8	7.4	9.6	32.2
Allowed to stand at R. T.	1.0	4.4	3.6	7.4	13.4	2.0	9.0	12.4	19.4	12.2

Each of approximately 100 cockroaches was treated with 125 micrograms of DDT in 2 microliters of acetone. They were held at 35° C. for 48 hours, and then transferred to 15° C. About 50 of the cockroaches were bled as they became prostrate, this blood constituting sample No. 1. The remainder were bled after they had been prostrate for 5 hours, this blood constituting sample No. 2. These samples were centrifuged, and the supernatants used in the experiment.

Both samples were assayed for toxic activity. Sample No. 1 caused marked increases, within 5 minutes, in spontaneous activity of all of the five cords on which it was assayed. Sample No. 2 did not cause any abnormally high activity to appear in 4 of the cords on which it was assayed, during a period of 30 minutes. In one cord a generally increased level of spontaneous activity appeared within 5 minutes after the cord was treated, and was maintained more or less constantly over a period of 30 minutes.

Both samples were allowed to stand for 3 hours at 27° C. At the end of this time they were reassayed.

Sample No. 1 had apparently lost all of its

toxic effects, none of the five cords on which it was assayed showing any definite signs of abnormally high activity within 30 minutes after they were treated. Sample No. 2, on the other hand, was definitely more effective in eliciting responses for cords. Trains of impulses appeared in four of the five cords treated within 10 minutes after treatment. In addition to the trains, there were marked increases in all levels of spontaneous activity. The fifth cord showed a sudden and violent increase in activity 13 minutes after it had been treated. The increased activity included high-frequency trains of large impulses, followed by a block of all activity.

Since the toxic effects disappeared from sample No. 1, and increased in sample No. 2 after standing for 3 hours at 27° C., it is apparently true that the toxin undergoes some sort of breakdown, or is otherwise inactivated under these conditions.

Stability of the toxin as dialysate.—Blood for this experiment was obtained from cockroaches treated with 125 micrograms of DDT in 2 microliters of acetone. They were held at 35° C. for 48 hours, and then transferred to 15° C. until all had been prostrate 3 hours. The blood was centrifuged and the toxicity of the supernatant verified by assaying it on several cords.

Several 50-microliter aliquotes of the supernatant were dialyzed, each against 250 microliters of physiological saline solution. The resultant dialysates were pooled, thoroughly mixed, and redivided into three equal aliquotes. The first was assayed for toxicity without any further treatment. The second was heated to 100° C. for 10 minutes, and then assayed for toxicity. The third was allowed to stand at room temperature (25° C.) for 3 hours, and then assayed. These results are presented in table 5.

A perusal of the data in table 5 might at first suggest that the heated dialysate, and that which was allowed to stand at room temperature, are both less toxic than the dialysate which was assayed without any previous treatment. All of the cords in the latter case, except cord No. 3, attained higher levels of activity than any of the cords in the other two cases. In view of the fact that variations occur between the responses of successive cords to treatment with aliquotes of the same blood sample; and further, as was pointed out earlier, since the method of quatating spontaneous activity used here is not entirely defining, this conclusion is probably not warranted. It is felt that the only conclusions that can reasonably be drawn are that all of the samples of dialysate assayed showed toxic activity, and that under the conditions of the experiment great losses in toxicity were not incurred.

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TWO NEW BLACK FLIES FROM THE WESTERN UNITED STATES (DIPTERA, SIMULIIDAE)[1]

ALAN STONE[2] AND G. R. DEFOLIART[3]

ABSTRACT

Simulium (*Simulium*) **petersoni** is described from Wyoming, Utah, and northern California, and *S.* (*Eusimulium*) **wyomingensis** from three localities in Wyoming.

We describe these species so that the names can be used in reporting the results of current biological and taxonomic studies.

[1]Published with approval of the Director, Wyoming Agricultural Experiment Station, as Journal Paper No. 124. The illustrations accompanying this paper were made by artists of the 406th Medical General Laboratory, U. S. Army, Japan, through the courtesy of Capt. Wallace F. Murdoch, MSC, and Col. Milward W. Bayliss, MC. Accepted for publication January 29, 1959.

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Simulium (Simulium) petersoni, new species

Female.—Frons nearly black, shiny, with a few fine pale hairs near eye margin, at narrowest about half as wide as width of one eye viewed from front. Antenna 11-segmented, almost uniformly dark. Clypeus dark, with a thin coating of grayish pollinosity. Mandibles and maxillae with the usual teeth. Palpus as figured (fig. 2) dark. Pharyngeal armature as figured (fig. 3). Thorax dark, subshining, with fine, recumbent, pale yellowish hairs on scutum, and longer, erect ones on scutellum. Viewed in certain lights, a pair of pale pollinose spots on scutum anteriorly; rest

of scutum unpatterned. Pleuron dark with thin grayish pollinosity; hairs of upper mesepimeron pale yellow. Legs (fig. 5): Entirely dark including fore coxa except for pale areas of the middle and hind tarsi, as shown; fore tibia and basitarsus distinctly flattened; calcipala small, acute; pedisulcus deep; claw untoothed, as figured (fig. 4). Wing: Length 2.5–2.75 mm.; hair of costa basad of humeral vein and on stem vein pale yellow; no hairs on subcosta ventrally; vein R bare above; vein R^1 with irregularly alternating short, fine hairs and heavier spines. Halter pale, the extreme base darkened. First abdominal tergite dark reddish brown, with pale yellow hair; tergites 2–5 dull blackish, 6–8 shining, nearly black, with fine pale hair. Terminalia as figured (fig. 7).

Male.—Holoptic, the upper facets much larger than the lower ones. Clypeus black with gray pollinosity and erect brownish hairs. Antenna and palpus black. Scutum dark, subshining, with fine, recumbent, brownish hairs and with a velvety black spot (white in certain lights) anteriorly on each side; most of scutum pale grayish by reflected light. Scutellum with erect brownish hair. Postnotum dark brown with grayish reflections; pleuron black, tinged with reddish; upper mesepimeral tuft yellowish. Leg coloration essentially as in female; hind basitarsus about 5.3 times as long as greatest width; calcipala very small. Wings and halteres as in female. First abdominal tergite dark with long pale yellow hairs; remaining tergites opaque black with rather long pale hairs laterally. Terminalia as figured (fig. 6).

Larva.—Length 5.5–6 mm. Frontoclypeus yellow-brown with an indistinct darker pattern as figured (fig. 8). Antenna 4-segmented, segment 2 with a submedian pale band. Throat cleft as figured (fig. 9); suboesophageal ganglion dark. Submentum (fig. 11) and tip of mandible (fig. 12) as figured. Mouth brushes with 60 to 70 filaments. Pupal respiratory histoblast as figured (fig. 10). Anal gills compound, each of the three divisions subdivided into 4 to 6 lobes. No ventral tubercles near end of abdomen.

Pupa.—Length 4 mm. Dorsum of head and thorax finely dark granulose. Head trichomes two on each side, fine, pale, close to antennal sheath; thoracic trichomes three on each side, very fine, pale, unbranched. Respiratory organ about 2 mm. long, with six filaments in pairs, each pair with rather short petioles or the middle pair nearly sessile (fig. 14). First tergite with two small, fine spines in transverse row near middle of each side; tergite 2 with six or seven fine spines or short hairs on each side; tergite 3 and 4 each with four stout, retrorse hooks in transverse row on each side near posterior margin; tergites 7–9 with irregular, short spines near anterior margin, those on 7 very small; tergite 9 with a pair of short, backwardly pointed, sclerotized teeth. Sternites 6–8 each with four hooklets, those on 6 bifid or trifid and paired, those on 8 evenly spaced. Cocoon (fig. 13) simple, with a very oblique anterior opening and a low projecting collar anteroventrally. Posterior half with a loosely woven floor.

Holotype, male with associated pupal skin, School Creek—N. Sybille Creek confluence, Albany Co., Wyoming, 18.VI.56 (G. R. DeFoliart). Paratypes, 1 female, 2 males with associated pupal skins, same data as holotype; male with associated pupal skin, 2.4 miles E. of Centennial, Wyoming, 12.VI.56 (DeFoliart); 3 males, Red Butte, Salt Lake Co., Utah, 22 and 26.VI.52 (B. V. Peterson); 40 larvae, 29 pupae, 7 pupal skins, 5 females, 2 males, Cedarville, Modoc Co., California, 29 and 30.VI.39 (T. H. G. Aitken); 1 female, 5 males, Alturas, Modoc Co., California VI.1948 (R. Coleman). Holotype in U. S. National Museum; paratypes in U. S. National Museum, University of Wyoming, University of Utah, and University of California.

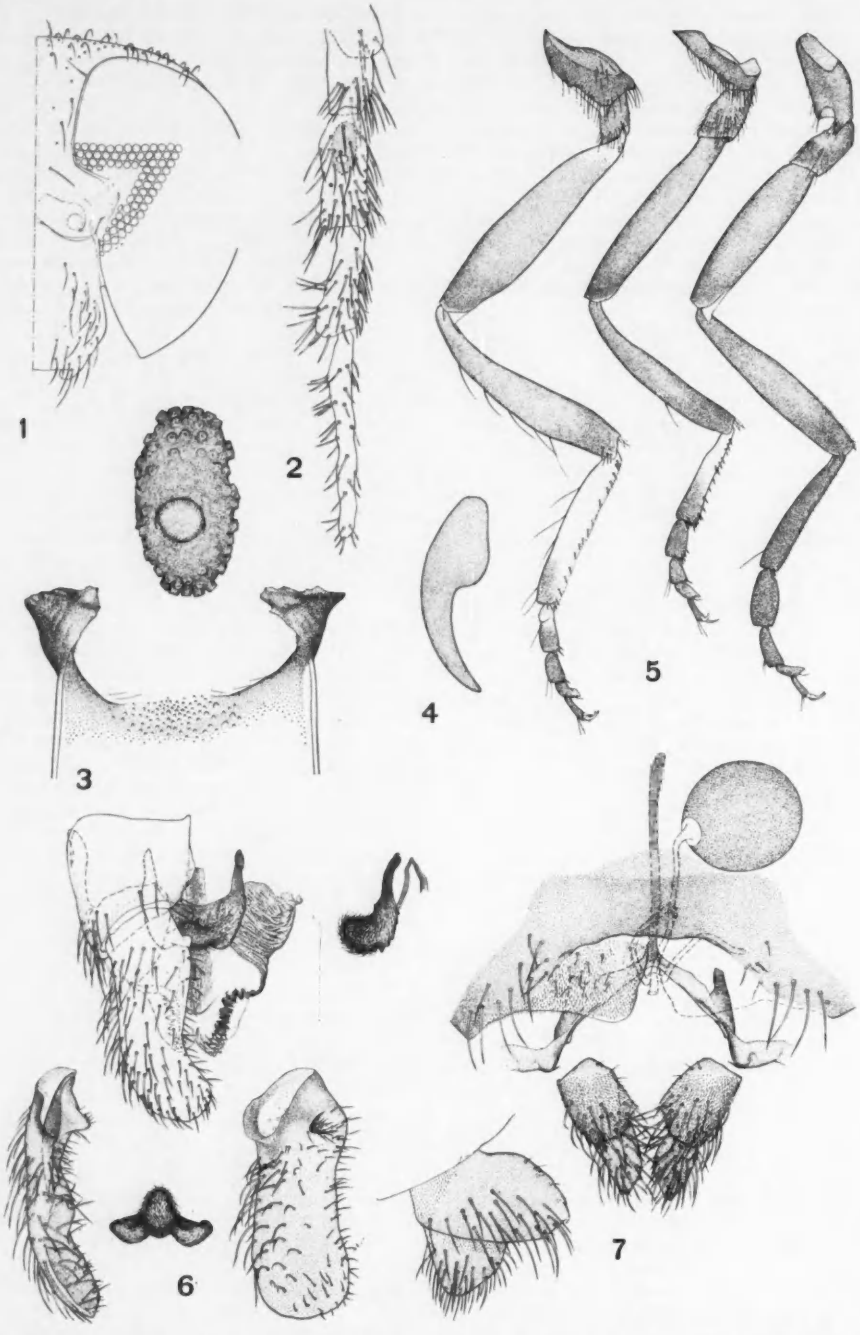
Other specimens presumably of this species are from Logan Canyon, Morgan, Daniel's Canyon, Willow Creek, and Cedar Brakes Nat. Mon., Utah, and Wiley and Yakima, Washington. These are not as positively determinable since they are not associated with immature stages, and we do not include them in the paratype series.

The female of this species can be distinguished from its nearest known relatives by the untoothed claws, dark fore coxae, and unstriped scutum. The male is close to *S. jacumbae* but the basal protuberance of the dististyle projects at right angles and does not point basad, and the dististyle is broader and flatter than in *jacumbae*. The larva resembles the eastern *S. parnassum*, but can be distinguished by the pale band on the second antennal segment and the smaller, more regular teeth on the submentum. The simple cocoon with a projecting anteroventral collar, will separate the pupa from other species with a similar respiratory organ.

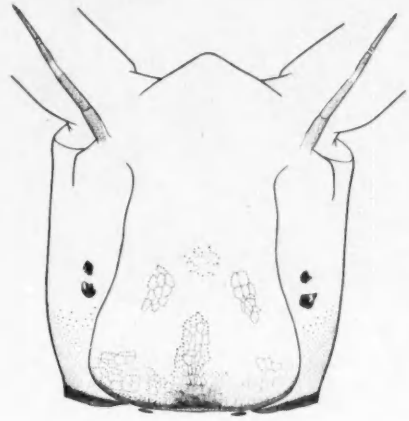
We take pleasure in dedicating this species to B. V. Peterson of the Entomology Laboratory, Department of Agriculture, Guelph, Ontario, able student of the family Simuliidae, who generously turned over to us a portion of the material of this species.

Simulium (Eusimulium) wyomingensis, new species

Female.—Frons gray pollinose, narrow, scarcely widened above, at narrowest about one-fourth as wide as width of one eye viewed from in front. Antenna 11-segmented, entirely dark. Clypeus dark with thin gray pollinosity and fine pale hairs. Mandibles and maxillae with the usual teeth. Palpus as figured (fig. 16). Thorax dark brownish-black, the scutum with fine silvery-white appressed hair, slightly tinged with yellowish discally, and with longer, erect hairs on scutellum; some grayish pollinosity around margin of



Simulium petersoni, n. sp. (1) Head of ♀; (2) palpus of ♀ and sensory organ enlarged; (3) pharyngeal armature of ♀; (4) claw of ♀; (5) hind, mid and fore legs of ♀; (6) male terminalia, ventral view, with details of dististyle and ventral plate; (7) female terminalia, ventral view, and lateral view of anal lobe and cercus.



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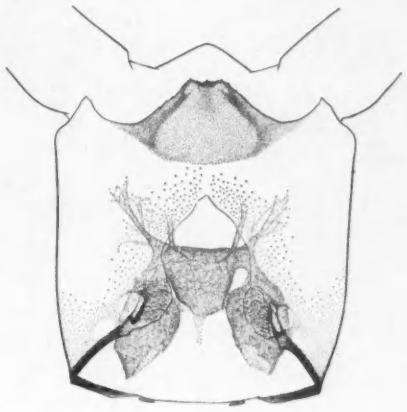

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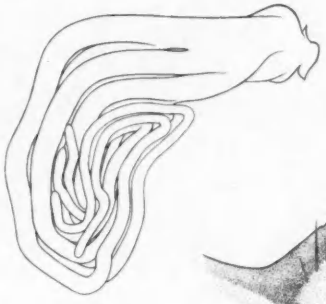

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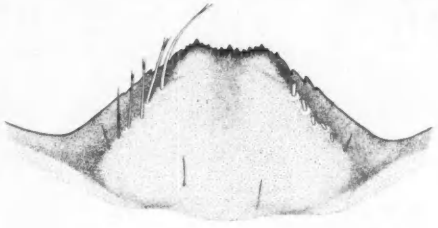

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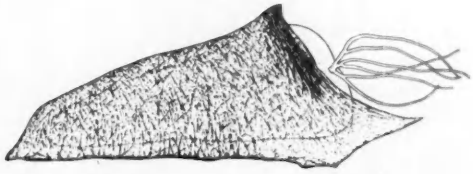

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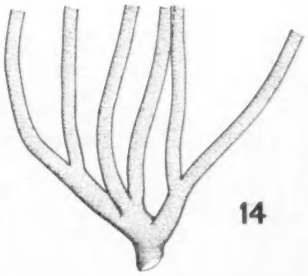

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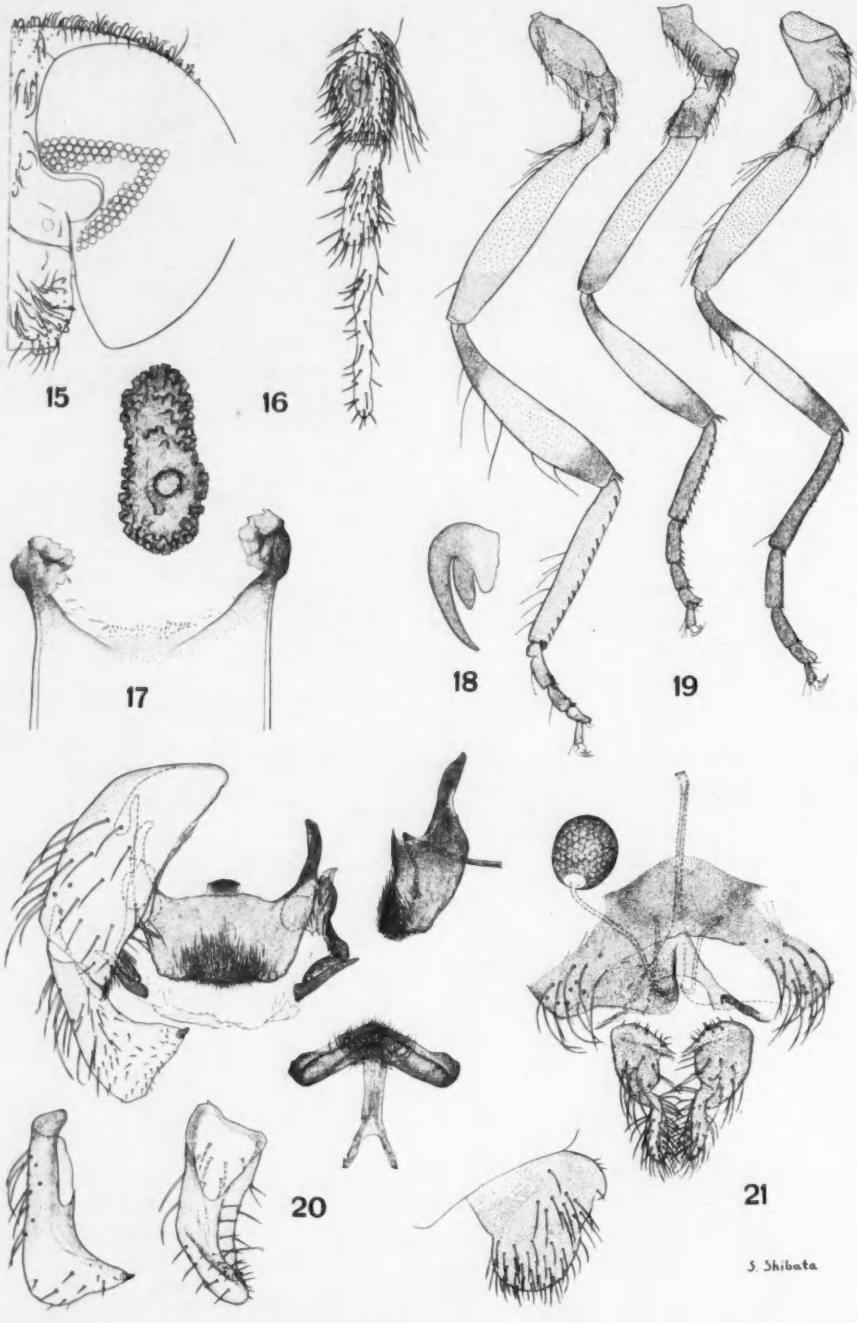
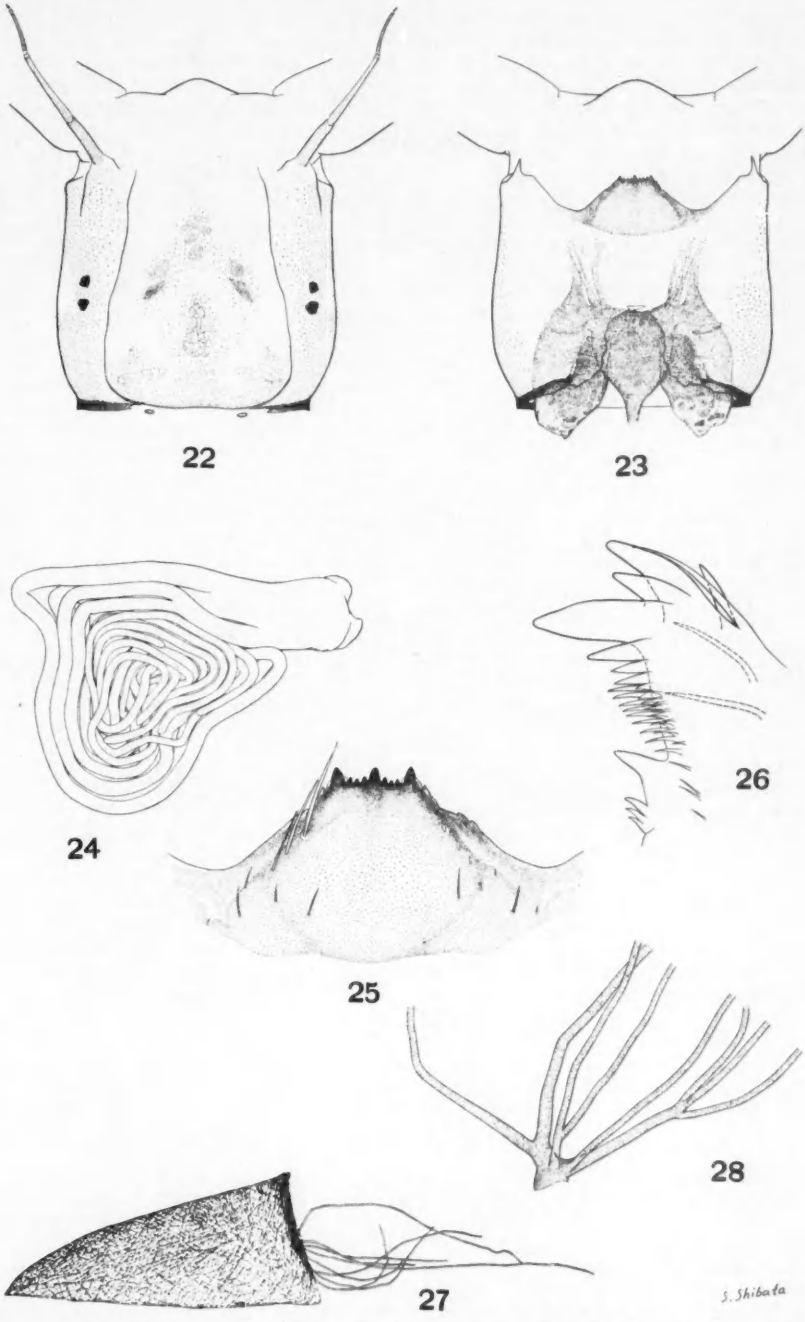
Simulium petersoni, n. sp. (8) Head of larva, dorsal; (9) head of larva, ventral view; (10) left respiratory histoblast of larva; (11) submentum of larva; (12) tip of mandible of larva; (13) cocoon and pupa, lateral view; (14) base of respiratory organ of pupa.



Simulium wyomingensis, n. sp. (15) Head of ♀; (16) palpus of ♀ and sensory organ enlarged; (17) pharyngeal armature of ♀; (18) claw of ♀; (19) hind, mid and fore legs of ♀; (20) male terminalia, ventral view, with details of dististyle and ventral plate; (21) female terminalia, ventral view, and lateral view of anal lobe and cercus.



Simulium wyomingensis, n. sp. (22) Head of larva, dorsal view; (23) head of larva, ventral view; (24) left respiratory histoblast of larva; (25) submentum of larva; (26) tip of mandible of larva; (27) cocoon and respiratory filaments of pupa, lateral view; (28) base of respiratory organ of pupa.

scutum. Pleuron dark with grayish pollinosity; no hairs on the reddish pleural membrane; hair tuft of upper mesepimeron pale yellow. Legs (fig. 19) dark, with paler yellowish areas as shown, these sometimes scarcely indicated; fore tibia and basitarsus distinctly flattened; hind basitarsus about six times as long as wide; calcipala rather small, pedisulcus deep; claw with a large basal tooth (fig. 18). Wing 2.5 to 2.75 mm. long; hairs of costa basad of humeral vein nearly white, those of stem vein dark; subcosta with a row of short hairs ventrally; vein R and vein R_1 with dark hair; radial sector with hairs beneath except near base. Halter pale, the extreme base darkened. Abdomen dark, with rather long pale hair, especially laterally; tergites subshining; sternites not sclerotized. Terminalia as figured (fig. 21), the anal lobe with a narrow ventral projection.

Male.—Holoptic, the upper facets much larger than the lower ones. Clypeus black, with erect dark hair. Antenna and palpus black. Scutum velvety black, with appressed, pale yellowish hair; hair of scutellum erect, pale. Pleuron as in female. Legs somewhat darker than usual for female; hind basitarsus somewhat enlarged; calcipala very small. Wing as in female, except that hairs along base of costa are dark. Halter dark reddish. Abdomen velvety black with dark hairs. Sternites developed except on second segment. Terminalia as figured (fig. 20).

Larva.—Length 6.5–7.0 mm. Frontoclypeus yellow-brown with pattern as figured (fig. 22). Antenna 4-segmented, the first and third segments slightly darker than the second. Throat cleft subquadrate, reaching nearly half way to base of mentum, with front rounded (fig. 23); suboesophageal ganglion slightly darkened. Submentum (fig. 25) and tip of mandible (fig. 26) as figured. Mouth brushes with about 55 filaments. Respiratory histoblast as figured (fig. 24). Anal gills three, each subdivided into 6–9 lobes. Ventral tubercles large, triangular.

Pupa.—Length 2.6–3.2 mm. Dorsum of head and thorax very slightly roughened. Head trichomes two on each side, very small; thoracic trichomes two on each side, pale, unbranched, of medium size. Respiratory organ (figs. 27, 28) as long as, or slightly longer than pupa, with eight filaments; two dorsal filaments widely diverging, others branching somewhat variably, in the holotype with the three lateral filaments almost sessile and the ventral petiole dividing and then the ventral branch dividing again farther out. Third and fourth tergites with four strong hooklets near posterior margin on each side; sixth with one or two, and seventh with four paler hooklets on each side near anterior margin; eighth with a row of about eight on each side near anterior margin; ninth with a pair of short black, acute, dorsally directed tubercles. Sternites 5–7 with four bifid hooklets on each, those on 5 in two pairs, those on 6 and 7 widely, almost evenly spaced. Cocoon (fig. 28) simple, rather broad, the opening nearly vertical the floor covering about posterior five-eights.

Holotype, male with associated pupal skin and cocoon, McGill Ranch irrigation ditch, Little Laramie River Valley, Albany Co., Wyoming, 10.VI.57 (G. R. DeFoliart). Paratypes: 11 females, 6 males, 16 pupal skins, 14 pupae and 33 larvae, same locality, 7–10.VI.57; 9 females, 6 males, 18 pupal skins, 27 larvae, 26 pupae, Middle Crow Creek, Blair Picnic Grounds, Albany Co., Wyoming, 3–6.VI.56 (DeFoliart); 30 females, 10 males, 48 pupal skins, 30 pupae, 4 larvae, Chalk Creek Canyon, Uinta Co., Wyoming, 31.V–2.VI.1956 (B. V. Peterson). Holotype in U. S. National Museum. Paratypes in U. S. National Museum, University of Wyoming, and University of Utah.

The female of this species can be separated from *S. canonicolum* and *S. crostoni* by the dark hairs on the stem vein and from *S. furculatum* by the strong basal, thumb-like projection of the claw. The male terminalia and the pupae are distinctive, the pupal filaments being much as in *furculatum* except for having the two of the dorsal pair widely divergent.

BOOK NOTICE

THE SCOLYTOIDEA OF THE NORTHWEST, by W. J. CHAMBERLIN. Oregon State College Monographs, Studies in Entomology, No. 2, 1958, 205 pp., 113 figs., $2.50.

This is the second extensive publication on this important group of insects by Dr. Chamberlin. The former one was photolitho offset in 1939 under the title: The Bark and Timber Beetles of North America. It contained 513 pages with many illustrations and an extensive bibliography. The present publication is essentially a condensation of the former work, with an elimination ot those species that do not occur in the Northwest. The first 30 pages or so are full of information on such subjects as types of galleries, biologies, lists of host plants, etc. Keys to subfamilies, genera and species, and treatment of individual species make up the bulk of the publication. Many helpful illustrations are included, some original, others taken from miscellaneous sources. There are some errors or deficiencies in the paper, but it is essentially a very good treatment of the species known to occur in the Northwest.

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Entomology Research Division,
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BIOLOGICAL NOTES ON THE SCALE INSECTS OF HUNGARY[1]

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ABSTRACT

Localities, collecting dates, and host-plant data are given for each of the 60 Hungarian species in the collection of the Academy of Horticulture and Viticulture in Budapest, and the known parasites of each are listed. The Hungarian scale fauna now totals 73 species, of which 16 are reported here for the first time. Some errors in the earlier Hungarian literature are corrected. Besides the systematic list of scales, an alphabetical list of more than 200 host plants is given, with their associated scale insects.

Fifty-seven scale-insect species were previously known from Hungary (with the exception of greenhouse scales, which are not discussed herein), and information concerning the geographical distribution and biology of these scales was incomplete. This paper, based on the extensive scale insect collection of the Academy of Horticulture and Viticulture in Budapest, provides additional information on the geographical distribution, host plants, degrees of infestation, and parasites of the scales of Hungary. During the years 1955–1956 approximately 1,000 microscope slides were prepared from this material. Sixty species of scales were identified, of which 16 species were new to the Hungarian fauna (these are marked with *). This brings the number of the known scales from Hungary to 73.

During the years 1954–1956 parasitological investigations of the scale insects of Hungary were conducted. Records of the parasites reared from the above-mentioned scale-insect material, plus previous references in the Hungarian literature, are listed under each scale species.

In this publication the Roman numerals following the host name indicate the degree of infestation.

(I) "Isolated infestation," when the scale insects occur individually and are few in number (fig. 5);

(II) "Medium infestation," when the scales cover less than one-third of the infested parts of the plant (fig. 1);

(III) "Heavy infestation," when the scale insects cover more than one-third of the infested parts of the plant (fig. 9);

(IV) "Layered infestation," when the scales completely cover the infested part of the plant (fig. 11).

Collecting dates are listed only when living material was collected. Many specimens were collected in the Arboretum of the Academy of Horticulture and Viticulture in Budapest, and this area has been indicated as Budapest: AAH.

[1]Accepted for publication November 18, 1958.

[2]Where no name is mentioned, the author was the collector; and when collections were made by the author jointly with another collector, the initials M. K. follow the other collector's name.

ACKNOWLEDGMENTS

I wish to thank all who have aided me by collecting scale insects, whose names are given in parentheses following locality data.[2] My thanks are due also to Dr. Eugene J. Gerberg, Director of Insect Control & Research, Inc., who encouraged me to publish this paper and who corrected my English translation; to Dr. B. D. Burks, U. S. National Museum, for checking the list of parasites; to Mr. E. C. Leonard, Smithsonian Institution, for checking the scale-insect host-plant list; and to Dr. Harold Morrison, Entomology Research Division, U.S.D.A., for reviewing the manuscript. Publication of the figures was made possible by a generous contribution from The Pinellas Foundation, Inc. Figure 6 is from a photograph by G. Jenser, and all other figures are from photographs by J. Lehoczky.

Family ORTHEZIIDAE

Orthezia urticae (L.). On *Achillea millefolium* L., Budapest: Gellérthegy (V. Martinovich), Pomáz: Kőhegy, Visegrád; on *Anthemis tinctoria* L., Csobánka: Hosszuhegy, Sept. 5, 1954; on *Artemisia campestris* L., Budapest: Sashegy, July 1950 (G. Balás and M. K.); a few larvae on *Cardaminopsis arenosa* (L.) Hayek, Budapest: Gellérthegy, Apr. 19, 1954 (V. Martinovich); larvae on *Dorycnium suffruticosum* var. *sericeum* (Neilr.) Beck, Pomáz: Kőhegy; larvae on *Euphorbia cyparissias* L., Csobánka: Hosszuhegy, Sept. 5, 1954, and one ♀ with several larvae, Pomáz: Kőhegy, Aug. 22, 1954; on *Filipendula hexapetala* Gilib., Budapest: Sashegy (G. Balás); larvae on *Galium pumilum* Murr., Csobánka: Hosszuhegy, Sept. 5, 1954; two ♀ ♀ and several larvae on *G. vernum* L., Pomáz: Kőhegy, Aug. 22, 1954; one ♀ and several larvae on *Odontites serotina* (Lam.) Dum., Pomáz: Kőhegy, Aug. 22, 1954; several ♀ ♀ on *Parietaria officinalis* L., Omasa in Bükk Mtns., July 21, 1953; isolated larva infestation on *Sanguisorba minor* Scop., Csobánka: Hosszuhegy, Sept. 5, 1954, and Kevélynyereg in Pilisi Mtns., May 2, 1955; one ♀ and several larvae on *Satureja vulgaris* (L.) Fritsch., Nagyhideghegy in Börzsöny Mtns., Sept. 27, 1953; larvae on *Teucrium chamaedrys* L., Budapest: Sashegy, Aug. 28, 1951 (G. Balás

and N. Tetmajer) and Csobánka: Hosszuhegy, Sept. 5, 1954; several ♀ ♀ and larvae on leaves and stem of *Urtica dioica* L., Abaujkér, Aug. 27, 1954, Bánkut: in Bükk Mtns., July 13, 1952, and Omasa, July 21, 1953.

***Newsteadia floccosa** (de Geer). One ♀ on moss, Köszeg, Apr. 6, 1955. According to Prof. E. Dudich, this species has been found several times on moss, in various parts of the country.

Family PSEUDOCOCCIDAE

Polystomophora ostiaplurima (Kir.). Several living ♀ ♀ on roadside trees of *Acer platanoides* L., Budapest, Aug. 24, 1955; on *A. pseudoplatanus* L., Budapest (G. Balás and M. K.); on *Aesculus hippocastanum* L., Budapest.

Parasite.—Encyrtidae: *Pseudaphycus hungaricus* Erdös (3).[3]

Chaetococcus phragmitis (March.). On *Phragmiles communis* Trin. (I), Békéscsaba (I. Joo), Érd (G. Balás, who collected from the reed material which was used in the construction of a building), Kelebia (J. Erdös and M. K.). Often parasitized.

Parasites.—Encyrtidae: *Asitus ciliatus* Erdös, *Boucekiella depressa* Hffr., *Platencyrtus parkeri* Ferr., *Platyrhopus meridionalis* (Ferr.), *Protyndarichus balatonicus* Erdös (5, 10).

Gossyparia spuria (Mod.) Isolated infestations were noted on the trunk, branches and twigs unless indicated otherwise. Usually in crevices in the bark. On *Ulmus americana* L., Sopron; on *U. glabra* Huds. (II), Bakonybél (fig. 1), Budapest: AAH. (G. Balás and M. K.), Klastrompuszta in Pilisi Mtns., Komárom (G. Balás), Magyarfalva (A. Terpo), Martonvásár, Nagymaros, Nográdveröce (S. Endrödi), Orosháza, Pécs, Sima in Borsod, Sopron, Szentendre, Visegrád; on *U. glabra* f. *exoniensis* (K. Koch) Rehd., Kecskemét (G. Balás), Szarvas; on *U. glabra* f. *pendula* (Loud.) Rehd., Zirc; on *Ulmus* sp., Budapest: AAH., Fenékpuszta in Veszprém, Kámon, Nagykevély in Pilisi Mtns., Szarvas, Tatatóváros kert (G. Balás and M. K.), Zalaszentgrot.

Parasites.—Encyrtidae: *Microterys feudatarius* (Merc.), *Trichomasthus coeruleus* Merc. (5). Miscogasteridae: *Pachyneuron coccorum* (L.) (16).

Acanthococcus aceris Sign. The most common scale on this host. Usually found in crevices in the bark of twigs and in the fork of branches (fig. 2) of *Acer campestre* L. In case of heavy infestation (Pomáz), the leaves were covered with the fungus *Apiosporium salicinum*. On *Acer campestre* L., Bakonybél, Budapest, Csobánka, Fertöd, Magyarkut in Börzsöny Mtns., Magyarovár, Martonvásár, Nyiregyháza (G. Jenser), Pomáz (Z. Baráth, A. Terpo, and M. K.); on *A. platanoides* L., Balatonföldvár, Tatatóváros kert (G. Balás and M. K.), Zirc.

Parasites.—Aphelinidae: *Coccophagus lycimnia* (Walk.); Encyrtidae: *Arrhenophagus chionaspidis* Aur., *Syrphophagus lineola* (Mayr) (5, 10).

***Acanthococcus roboris** (Goux). Isolated infestations on trunk and branches (particularly close to the ground) of *Quercus cerris* L., in Börzsöny Mtns.: Magyarkut, Nagyhideghegy, Nagymaros; on *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy, Csobánka: Hosszuhegy, Magyarkut; on *Q. pubescens* Willd., Leányfalu, Pécs: Misinatetö.

Parasites.—Encyrtidae: *Microterys chalcostomus* (Dalm.), *Trichomasthus niveicrus* Erdös (4, 5).

Rhizococcus obscurus Borchs. Several ♀ ♀ at the base of leaves of *Agropyron intermedium* (Host.) Beauv., Pomáz: Kiscsikovár (A. Terpo). Often parasitized (fig. 3).

Parasites.—Aphelinidae: *Marietta zebra* Kurdj. (hyperparasite). Thysanidae: *Xana kurdjumovi* Nik. (possible hyperparasite). Encyrtidae: *Aphycus nitens* Kurdj., *Coccidencyrtus breviventris* (Kurdj.), *Parasyrphophagus lindus* Merc. (5, 10).

Pseudochermes fraxini (Kalt.). Often heavy infestations on trunk and branches. On *Fraxinus excelsior* L., Balatonszentgyörgy, Budapest: Margitsziget (G. Balás) and Szabadsághegy, Köszeg (A. Terpo), Martonvásár (S. Kaszonyi and M. K.), Pomáz: Kiscsikovár and Köhegy, Zirc in park; on *F. ornus* L., Csobánka: Hosszuhegy (fig. 4), Holdvilágárok in Pilisi Mtns., Magyarovár, Nagymaros: Hegyestetö, Solymár, Szentendre; on *Fraxinus* sp., Gödöllö, Mátraháza.

Cryptococcus fagisuga Lndgr. On trunk of *Fagus sylvatica* L. (I), Badacsony, Fertöd, Gézaháza in Blakony Mtns., Gönc, Kétbükkfanyereg and Lajos-forrás in Pilisi Mtns., Ördögárok in Bakony Mtns., Visegrád; on *F. sylvatica* f. *atropunicea* (West.) Domin, Zirc in park.

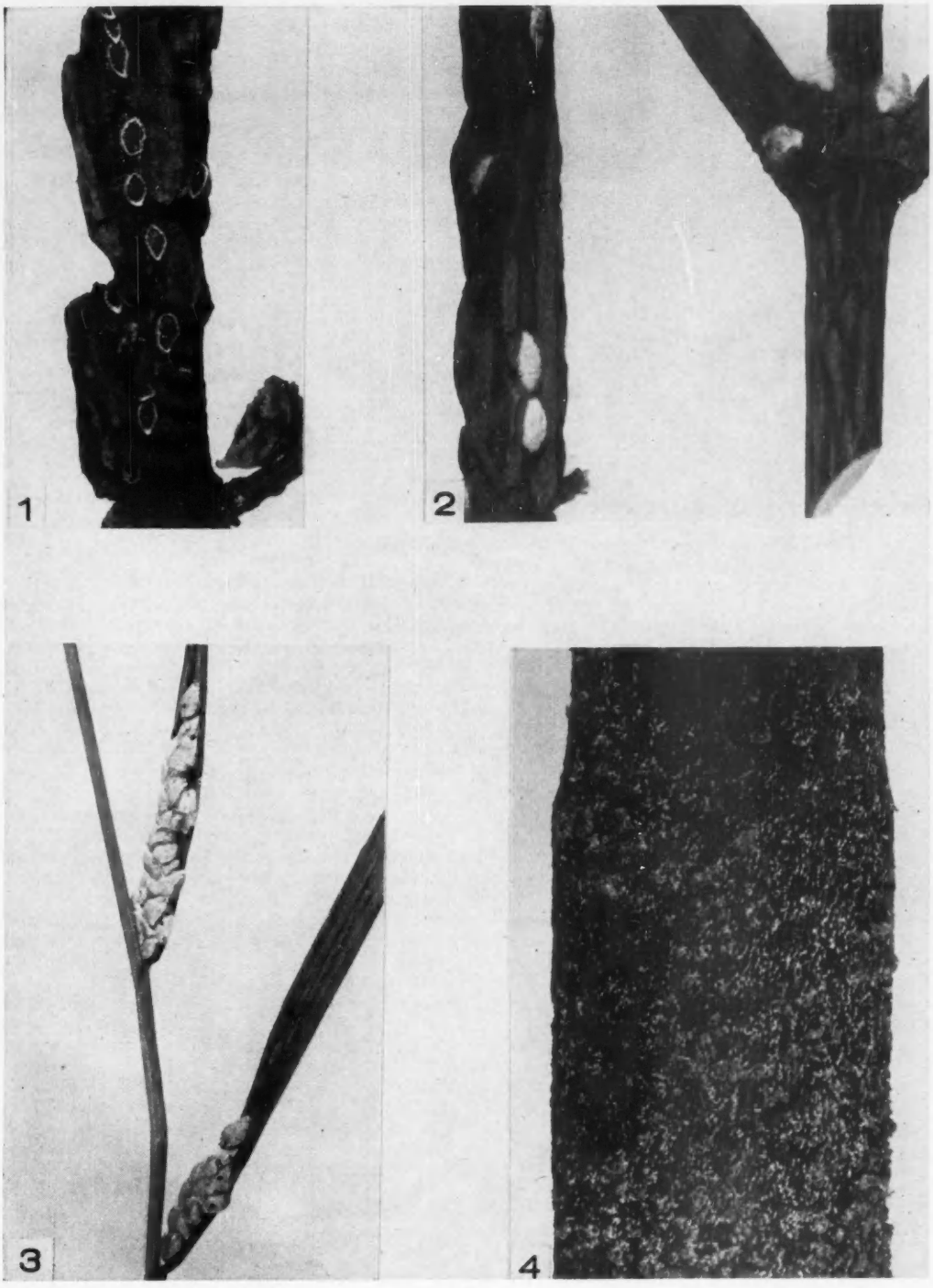
Family KERMOCOCCIDAE

Kermococcus quercus (L.). Isolated infestations on trunk and branches. On *Quercus petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy (G. Balás); on *Q. robur* f. *fastigiata* (Lam.) Schwarz, Szarvas: Arboretum.

[3]Arabic numbers in parentheses refer to the bibliographic items listed at the end of the paper.

EXPLANATION OF PLATE I

FIG. 1.—*Gossyparia spuria* (Mod.), females on a twig of *Ulmus glabra* Huds. FIG. 2.—*Acanthococcus aceris* Sign., females in crevices in bark of a twig and in fork of a branch of *Acer campestre* L. FIG. 3.—*Rhizococcus obscurus* Borchs., egg sacs on leaves of *Agropyron intermedium* (Host.) Beauv. Some are parasitized. FIG. 4.—*Pseudochermes fraxini* (Kalt.), females on trunk of *Fraxinus ornus* L.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Parasites.—Encyrtidae: *Microterys chalcostomus* (Dalm.), *M. ferrugineus* (Nees) (5).

Kermococcus roboris (Fourc.). Isolated infestations on trunk and branches. On *Quercus cerris* L., Budapest: Hűvösvölgy, June 5, 1955, and Látohegy, Holdvilágárok in Pilisi Mtns.; on *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hűvösvölgy, Csobánka: Hosszuhegy; on *Q. pubescens* Willd., Fánivölgy in Vértes Mtns., Pomáz: Kiscsikovár; on *Q. robur* L., Veszprém. Often parasitized (fig. 5).

Parasite.—Encyrtidae: *Blastothrix erythrostethus* (Walk.) (5).

Family Asterolecaniidae

***Asterolecanium arabidis** (Fonsc.). Isolated infestations. On stem of *Achillea millefolium* L., Komárom, Aug. 1942 (G. Balás); on stem, leaves, and petioles of *Hedera helix* L. The infested part of plant may become thick and gall-like (fig. 6). Ivy in forests was examined several times, but no coccids were observed. Badacsonyörs, Budapest: AAH., Gellérthegy (Z. Gelencsér and I. Kiss), Kőbánya (E. Sághelyi), Csáford in Zala, Eger, Kecskemét (G. Balás), Keszthely, Mátészalka, Nagymaros, Orosháza (I. Joo and M. K.), Szigliget (V. Kőfarago-Gyelnik), Tatabánya; on twigs of *Ligustrum vulgare* L., where it caused thickening, Budaörs: Kamaraerdő (J. Domokos and M. K.), Budapest: AAH. (G. Balás and M. K.); on stem of *Lithospermum purpureocoeruleum* L., where it caused thickening, Budaörs: Kamaraerdő.

Parasites.—Encyrtidae: *Cheiloneurus kollari* Mayr, *Discodes aeneus* (Dalm.), *D. cercopiformis* (Walk.) (5).

Asterolecanium bellum Rsl. Isolated infestations on branches and twigs. On *Quercus cerris* L., Budapest: Hűvösvölgy, Fánivölgy, Magyarkut, Nagymaros, Pécs: Misinatető, Pomáz: Kiscsikovár, Türje in Zala; on *Q. lyrata* Walt., Kámon in Vas; on *Q. pubescens* Willd., Budaörs: Kamaraerdo (G. Balás).

***Asterolecanium minus** Lndgr. Isolated infestations on branches and twigs. Thickening of branches resulted. On *Quercus cerris* L., Budapest: Szabadsághegy, Nagymaros; on *Q. lyrata* Walt., Kámon; on *Q. petraea* (Matt.) L. ex Liebl., Bakonybél, Budapest: Hűvösvölgy and Margitsziget (G. Balás), Bükköspatak in Pilisi Mtns., Kőszeg; on *Q. pubescens* Willd., Budapest: Hűvösvölgy, Leányfalu, Monori-erdő, Sima; on *Q. robur* L., often heavy infestations, Békéscsaba (G. Balás and I. Joo), Budapest: Kőbánya, Margitsziget (G. Balás), and Tabán (Gy. Méhes), Kecskemét, Szarvas: Arboretum, Szeged in Botanical Garden, Veszprém.

Parasites.—Encyrtidae: *Aphycus intermedius* Merc., *Habrolepis dalmani* Westw. (5).

***Asterolecanium quercicola** (Bouché). One ♀ on a twig of *Quercus petraea* (Matt.) L. ex Liebl., Kőszeg: Kálvária.

***Asterolecanium roboris** Rsl. Two ♀♀ on a twig of *Quercus pubescens* Willd., Leányfalu.

Asterolecanium variolosum (Ratz.). Caused thickening of branches and twigs. On *Quercus cerris* L. (I), Holdvilágárok; occasionally medium infestations on *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hűvösvölgy and Margitsziget (G. Balás), Bükköspatak, Kőszeg; on *Q. petraea* f. *laciniata* (Lam.) Schwarz (I), Budapest: AAH. (G. Balás); on *Q. pubescens* Willd. (I), Balatonfüred (I. Joo); occasionally heavy infestations on *Q. robur* L., Budapest: Kőbánya and Margitsziget, Eger, Gézaháza, Győr, Magyarovár, Nagykállo, Orosháza, Tihany; on *Q. robur* f. *concordia* (Kirchn.) K. Koch (I), Zirc in park; one ♀ on *Q. rubra* L., Sopron in park.

Parasites.—Encyrtidae: *Habrolepis dalmani* Westw., *H. pascuorum* Merc. (5, 10).

Family Coccidae

Eriopeltis festucae (Fonsc.). On the leaves of *Agropyron repens* (L.) Beauv. (I), Ágasegyháza (G. Balás), Budapest: AAH. Often parasitized.

Parasites.—Ephydridae (Diptera): *Leucopis annulipes* Zett. (2, 10). Encyrtidae: *Baeocharis pascuorum* Mayr, *Subprionomitus cantabricus* Merc., *Trichomasthus cyanifrons* (Dalm.) (5). Miscogasteridae: *Pachyneuron coccorum* (L.) (16).

Eulecanium arion (Lndgr.). On twigs and shoots of *Thuja occidentalis* L. (I), Zirc in park.

Parasite.—Miscogasteridae: *Asaphes vulgaris* (Walk.) (questionable as parasite of scales) (10).

Eulecanium bituberculatum (Targ.). Isolated infestations on branches and twigs. On *Crataegus monogyna* Jacq., Budaörs: Kamaraerdő, Csobánka; on *C. oxyacantha* L., Budaörs: Kamaraerdő: on *Crataegus* sp., Nagymaros; on *Malus pumila* Mill., Sopron.

***Eulecanium ciliatum** (Dougl.). Four ♀♀ on twigs of *Juglans regia* L., Pécs.

Eulecanium corni (Bouché). One of the most common scales in Hungary and an important pest of fruit and forest trees, particularly black locust. Hungarian literature (G. Horváth, J. Jablonowski, and K. Sajo) states one yearly generation in discussing the biology of this scale. The author

EXPLANATION OF PLATE II

Fig. 5.—*Kermococcus roboris* (Fourc.), females on twigs of *Quercus cerris* L. The female marked with an arrow is parasitized. Fig. 6.—*Asterolecanium arabidis* (Fonsc.), females on leaves and petioles of *Hedera helix* L. The infested leaves are deformed, and their petioles become thick and gall-like. Fig. 7.—*Eulecanium corni* (Bouché), male scales on a twig of *Populus nigra* var. *italica* (Münchh.) Koehne. Fig. 8.—*Eulecanium rufulum* Ckll., females on a twig of *Quercus cerris* L.

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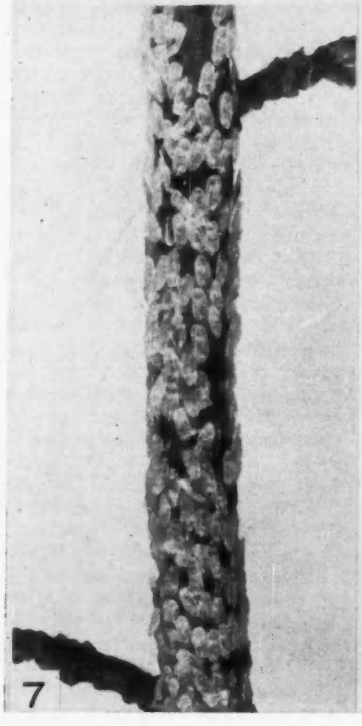

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observed the second generation in Tompa (South Hungary) on Sept. 5, 1955. In addition to the old, dried females of the first generation, several egg-laying adults were seen at this time. On the same day, in the neighboring town of Kelebia, several male scales were collected on poplar trees (*Populus* sp.) (J. Erdös and M. K.). This material yielded winged males after 4 days. The control examinations of the following year (1956) indicated that this scale has two yearly generations in South Hungary.

Isolated infestations were noted on twigs and branches, unless indicated otherwise. On *Acer negundo* L., Budapest: AAH. (G. Balás and M. K.), Kecskemét, Kisvárda (A. Terpo), Lillafüred, Mátészalka; on *A. negundo* var. *odessanum* H. Rothe, Budapest: AAH.; on twigs of *A. pseudo-platanus* L., Martonvásár in park (I. Nyékes), Szarvas: Arboretum; a few male scales on *Aesculus hippocastanum* L., Martonvásár in park; on *A. pavia* L., Budapest: AAH.; on *Amorpha fruticosa* L., Budapest: AAH., Jászberény; on *Broussonetia papyrifera* (L.) L'Hérit, Kiskunhalas; on *Buxus sempervirens* L., Budapest: AAH.; on *Campsis radicans* (L.) Seem., Budapest: AAH. (G. Balás), Helvécia (I. Zelena); on *Caragana arborescens* Lam., Budapest: AAH., Köszeg (T. Pomogyi), Orosháza, Szombathely, Tatatóvároskert (G. Balás and M. K.); on *Carpinus betulus* L., Budapest: AAH. (G. Balás); on *Celtis australis* L., Jászberény, Sopron; on *C. occidentalis* L., Budapest: AAH. (G. Balás), Fényeslitke (A. Terpo), Magyarovár, Orosháza, Szarvas: Arboretum, Tatatóvároskert (G. Balás and M. K.), Vácrátot (A. Andrásfalvy); on *Cercidiphyllum japonicum* S. et Z., Zirc in park; on *Cercis siliquastrum* L., Buadpest: AAH., Pécs: Balokány; on *Clematis vitalba* L., Budaörs: Kamaraerdö (G. Balás); on *Colutea arborescens* L., Jászberény; heavy infestation on *Cornus mas* L., Erdöbénye (A. Terpo), isolated infestations: Gönc, Martonvásár in park, Nyiregyháza (G. Jenser); on *C. sanguinea* L., Balatonfüred, Fenékpuszta; male scales too on *Corylus avellana* L., Budaörs: Kamaraerdö (G. Balás, E. Horn, and M. K.), Jászberény, Szarvas: Arboretum, Visegrád; on *Cotoneaster acutifolia* Turcz., Budapest: AAH.; male scales too on *Crataegus monogyna* Jacq., Budaörs: Kamaraerdö, Csobánka; on *C. orientalis* Pall., Szarvas: Arboretum; on *C. oxyacantha* L., Budaörs: Kamaraerdö, Budapest: AAH and Hüvösvölgy (layered infestation of male scales), Zsujta in Borsod; medium infestation on *Crataegus* sp., Nagymaros; one parasitized ♀ on *Cudrania tricuspidata* (Carr.) Bureau, Kámon (I. Joo); on *Cydonia oblonga* Mill., Ágasegyháza, Sasad (M. Macher), Vecsés (B. Szabo); on *Elaeagnus angustifolia* L., Jászberény; on *Fraxinus excelsior* L., Bánkut (B. Ambrus), Budapest: Lipotmezö (G. Balás and M. K.), Dabas (A. Terpo), Tinnye, Zsujta (A. Terpo); on *F. excelsior* f. *pendula* Ait. Schelle, Zirc in park; heavy infestations on branches and twigs of *Fraxinus* sp., Hatvan, Martonvásár (males also), Miskolc (Gy. Toth); on *Gleditschia triacanthos* L., Nyiregyháza: Sosto (A. Terpo), Tatatóvároskert (G. Balás and M. K.); on *Juglans regia* L., Budaörs: Kamaraerdö (G. Balás), Mezötur, Nagygombos, Pécs, Sárhely (A. Terpo), Szombathely, Visegrád; on *Lonicera tatarica* L., Budapest: AAH., Jászberény; on *Maclura pomifera* (Raf.) Schneider, Debrecen; often heavy infestations on branches of *Morus alba* L., Fánivölgy, Gyöngyös (J. Domokos), Magyarovár, Monorierdö, Nagymaros; on *Parthenocissus tricuspidata* (Sieb. et Zucc.) Planch., Törökbálint (K. Magyar); on *Platanus occidentalis* L., Tatatóvároskert; on *P. orientalis* L., Kecskemét, Sopron (N. Tetmajer and M. K.); layered infestations of male scales on twigs and leaves of *Populus nigra* var. *italica* (Münchh.) Koehne (fig. 7), Budapest: Népliget, Mátraháza, Szeged, Tatatóvároskert (G. Balás and M. K.); on *Prunus amygdalo-persica* (West.) Rehd., Budapest: AAH., on *P. amygdalus* Batsch., Budapest: Farkasvölgy (A. Terpo), Törökbálint (K. Magyar); on *P. armeniaca* L., Szár in Vértes Mtns.; medium infestation of male scales on twigs of *P. avium* L., Zsujta (A. Terpo); on *P. cerasifera* var. *atropurpurea* (Jaeg.) Rehd., Budapest: AAH.; the most common scale on *P. domestica* L. Often heavy infestations on branches and twigs. The scales produce large quantities of honeydew, on which the fungus *Apiosporium salicinum* flourishes, covering the leaves with a black coating. This coating interferes with photosynthesis, causing a reduction in the sugar content of the fruit. Budapest: Gellérthegy and Hüvösvölgy, Csenger (G. Jenser), Erdöbénye (A. Terpo), Gönc (males also), Mád (Gy. Toth), Miskolc (Gy. Toth), Nagygombos, Nográdveröce (males also, S. Endrödi), Pilisborosjenö (V. Martinovich), Piliscsaba (A. Terpo), Pomáz (M. Faust), Szár, Szentendre (V. Martinovich), Törökbálint (K. Magyar), Tura, Visegrád; on *P. padus* L., Martonvásár in park (males also); on *P. persica* (L.) Batsch., Esztergom (E. Horváth), Visegrád; often heavy infestations on *P. spinosa* L., Budaörs: Kamaraerdö, Budapest: Hüvösvölgy (G. Balás), Keszthely, Pomáz: Köhegy (males also), Zsujta (A. Terpo); on *Pyracantha coccinea* Roem., Budapest: AAH.; on *Pyrus communis* var. *pyraster* L., Köszegdoroszlo (A. Terpo); on *P. communis* var. *sativa* (DC.) DC., Dánszentmiklos, Kerepes (layered male infestation, E. Probocskai), Nagymaros; on *Ribes aureum* Pursh., Kisvárda (A. Terpo); on *R. grossularia* L., Budaörs: Kamaraerdö (males also), Fertöd (S. Kaszonyi), Nagymezö in Bükk Mtns., Szentendre; on *R. nigrum* L., Balatonszéplak (males also); on *R. rubrum* L., Budapest: AAH. and Kispest; often layered infestations on branches and twigs of *Robinia pseudacacia* L. causing damage. Ágasegyháza, Budaörs: Csiki Mtn. (Z. Baráth and A. Terpo), Eger, Egervár in

Zala (a large number of larvae were on the leaves on Sept. 23, 1955), Felsögöd (A. Andrásfalvy), Gödöllö (F. Bakk), Herceghalom (L. Tohai), Herény in Vas, Jászberény, Kisvárda (A. Terpo), Mátészalka, Mezötur, Miskolc (Gy. Toth), Monorierdö, Nagymaros, Nográdveröce (S. Endrödi), Ocsa (E. Zsentko), Sopron, Szarvas: Arboretum, Szombathely, Tatatóváraskert (G. Balás and M. K.), Telkibánya in Borsod, Tihany (J. Domokos), Tinnye, Vasboldogasszony (L. Tohai), Visegrád, Zalaszentgrot, Zebegény: Kövesmezö; on *Rosa canina* L., Budaörs: Kamaraerdö; on *Rosa* sp., Budaörs: Kamaraerdö, Budapest: Gellérthegy, Pécs (male scales also); on *Rubus* sp., Budaörs: Kamaraerdö (G. Balás); heavy male infestation on *Salix candida* Flügge ex Willd., Kámon; often several male scales on *Salix* sp., Gerencevölgy in Bakony Mtns., Tata-Bánya, Zalaszentgrot; male scales also on *Sambucus nigra* L., Martonvásár in park; on *Sophora japonica* L., Budapest: AAH. and Szépvölgy (G. Balás), Jászberény, Kisvárda (A. Terpo), Mezötur, Szarvas: Arboretum; on *Symphoricarpus albus* (L.) Blake, Jászberény, Nagymaros; on *S. albus* var. *laevigatus* (Fern.) Blake, Budapest: Szépvölgy (V. Martionovich); on *Tamarix gallica* L., Budapest: AAH. (G. Balás and M. K.), and Kispest; male scales also on *Tamarix* sp., Budapest (M. Nádor); male scales also on *Tilia cordata* Mill., Tatatóváraskert; on *T. platyphyllos* Scop., Szarvas: Arboretum; often male scales also on *Tilia* sp., Köszeg, Pécs, Szombathely, Tatatóváraskert (G. Balás and M. K.), Visegrád; on *Ulmus glabra* f. *atropurpurea* (Späth) Rehd., Budapest: AAH. (G. Balás); several larvae on leaves of *U. glabra* f. *exoniensis* (K. Koch) Rehd., Szarvas: Arboretum, Oct. 15, 1950; male scales also on *U. glabra* f. *pendula* (Loud.) Rehd., Zirc in park; on *Ulmus* sp., Budapest: Lipotmezö (G. Balás), Kámon, Mezötur, Szarvas: Arboretum; occasionally medium infestations on grapes in arbors (*Vitis vinifera* L.), Badacsony (V. Martinovich), Besenyszög near Szolnok, Békéscsaba, Budaörs, Budapest: Kispest, Obuda (M. Gianonne and A. Hegedüs), and Pestszentlörinc (Gy. Mende), Maglod (A. Boros), Martonvásár (K. Bartik), Mezöberény (Á. Ványai), Ocsa (E. Zsentko), Pomáz: Kiscsikovár, Rétság in Nográd (G. Jenser), Szöny (I. Teke), Törökbálint (J. Semetke), Visegrád (male scales also).

Predators.—Coccinellidae: *Exochomus quadripustulatus* (L.). Anthribidae: *Brachytarsus fasciatus* Forster, *B. nebulosus* Forster (8, 12).

Parasites.—Aphelinidae: *Coccophagus lycimnia* (Walk.), *C. scutellaris* (Dalm.). Encyrtidae: *Cerapterocerus mirabilis* Westw. (hyperparasite), *Metaphycus insidiosus* (Merc.), *M. parvus* (Merc.), *Pezaphycus obenbergeri* Novicky. Eupelmidae: *Eupelmus urozonus* Dalm. Miscogasteridae: *Pachyneuron coccorum* (L.). (5, 6, 9, 10).

Eulecanium coryli (L.). On branches and twigs of the host. A few ♀ ♀ on *Acer pseudoplatanus* L., Fertöd, Sopron; one ♀ on *A. saccharinum* L., Pomáz; on *Aesculus hippocastanum* L. (I), Budapest: Lipotmezö (G. Balás and M. K.), and Népliget, Fertöd (male scales also), Fenékpuszta, Keszthely, Pomáz, Sopron (male scales also), Szalajka-völgy (male scales also); two ♀ ♀ on *Cornus sanguinea* L., Budaörs: Kamaraerdö; a few ♀ ♀ on *Corylus avellana* L., Szarvas: Arboretum; on *Crataegus monogyna* Jacq. (I), Budaörs: Kamaraerdö (male scales also); on *C. oxyacantha* L. (I), Budaörs: Kamaraerdö, Budapest: AAH. (Á. Ványai); three ♀ ♀ on *Malus pumila* Mill., Sopron; male scales also on *Prunus domestica* L. (I), Budaörs: Kamaraerdö (G. Balás), Piliscsaba (A. Terpo); isolated infestations on *Quercus petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy (L. Boross), Gödöllö (one male scale also), Holdvilágárok, Nagymaros: Hegyestetö; heavy infestation of young females and male scales on *Rosa spinosissima* L., Nadap: Meleghegy, May 15, 1952 (G. Balás), one ♀ on *Rosa* sp., Budaörs: Kamaraerdö; one ♀ on *Tilia cordata* Mill., Tatatóváraskert; on *Tilia* sp. (I), Gödöllö and Herény (only male scales), Visegrád.

Parasites.—Aphelinidae: *Coccophagus scutellaris* (Dalm.) (6). Encyrtidae: *Blastothrix sericea* (Dalm.), *Metaphycus mayri* (Timb.), *Microterys sylvius* (Dalm.) (5, 7).

Eulecanium crudum Green. On twigs of *Taxus baccata* L. (I), Kámon, Szarvas: Arboretum, Tatatóváraskert (G. Balás and M. K.), Zalaszentgrot, June 6, 1955 (M. Fehér).

Parasites.—Aphelinidae: *Coccophagus lycimnia* (Walk.). Encyrtidae: *Aphycus parvus* Merc., *Metaphycus insidiosus* (Merc.) (5, 10).

***Eulecanium franconicum** (Lndgr.). Two ♀ ♀ on a twig of *Calluna vulgaris* (L.) Hull, Köszeg.

Eulecanium persicae (F.). The author never collected this scale on peach trees, and did not find it from peach in the extensive *Eulecanium persicae* material of the Hungarian National Museum. The author believes that the records in the Hungarian literature concerning *Eulecanium persicae* damage to peach trees probably are based on incorrect identifications. On peach trees, the plum scale, *Eulecanium prunastri* (Fonsc.), was noted as common in Hungary.

On a twig of *Berberis vulgaris* L. (I), Tatatóváraskert (G. Balás and M. K.); on twigs of *Parthenocissus tricuspidata* (Sieb. et Zucc.) Planch. (III), Budapest: Kispest, May 28, 1955 (A. Korschelt and M. K.) and Lajos-utca (L. Dörgö).

Parasites.—Encyrtidae: *Aphycus parvus* Merc., *Blastothrix sericea* (Dalm.), *Microterys sylvius* (Dalm.) (5, 7, 10, 15).

Eulecanium prunastri (Fonsc.). This scale is reported in Hungarian literature as the most common scale attacking plum trees. It was found to be uncommon on fruit plums (*Prunus domestica* L.), but very common on orna-

mental plums. Another scale, *Eulecanium corni* (Bouché), was noted as an important pest of fruit plums.

On branches and twigs. On *Prunus amygdalus* Batsch. (I), Nagymaros; on *P. armeniaca* L., Ágasegyháza (male scales also), Budaörs: Kamaraerdő (G. Balás), Budapest: Kispest (I. Nyékes); on *P. baldschuanica* Reg., Budapest: AAH.; male scales also on *P. cerasifera* Ehrh., Budapest; AAH. and Tiszalök; often heavy infestations with male scales also on *P. cerasifera* var. *atropurpurea* (Jaeg.) Rehd. Often are parasitized on this host. Balatonfüred, Békásmegyer, Budapest: Budagyöngye (D. Suhajda) and Budapest: AAH.; Nagymaros, Pécs, Zalaszentgrot in park; on *P. domestica* L. (I), Rákosszentmihály (L. Jezerniczky), Szilvásvárad, Visegrád; occasionally heavy infestations on *P. persica* (L.) Batsch., Budaörs: Kamaraerdő (A. Terpo), Budapest: Kispest, Nagymaros, Perbál (S. Sebestyén), Tatabánya; often heavy infestations (male scales also) on *P. spinosa* L., Budaörs: Kamaraerdő, Budapest: Testvérhegy, Leányfalu, Peskő in Bükk Mtns., Türje.

Parasites.—Aphelinidae: *Coccophagus lycimnia* (Walk.), *C. scutellaris* (Dalm.), *Pteroptrix maritima* Nik. Encyrtidae: *Cerapterocerus mirabilis* Westw., *Discodes aeneus* (Dalm.) and a hyperparasite therefrom, *Metaphycus punctipes* (Dalm.), *Microterys hortulanus* Erdös. Miscogasteridae: *Pachyneuron coccorum* (L.). (3, 5, 10).

Eulecanium rufulum Ckll. On twigs and branches. Isolated infestations on *Castanea sativa* Mill., Budaörs (G. Balás), Köszeg, heavy infestations at Nagymaros and Pomáz; on *Corylus avellana* L. (II), Erdőbénye (A. Terpo); five ♀ ♀ on *Elaeagnus angustifolia* L., Nyiregyháza (G. Jenser); on *Loranthus europaeus* Jacq. (II), Leányfalu; on *Quercus alba* L. (II), and on *Q. castaneifolia* C. A. Meyer (II), Szarvas: Arboretum (N. Tetmajer); often heavy infestations on *Q. cerris* L. (fig. 8), Bakonybél, Holdvilágárok, Kisinoc in Börzsöny Mtns., Pomáz: Kiscsikovár, Szalajka-völgy and Szarvaskő in Bükk Mtns. (D. Suhajda), Veszprém; on *Q. palustris* Münch. (II), Szarvas: Arboretum (N. Tetmajer and M. K.); often heavy infestations on *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy (G. Balás and M. K.), Csobánka: Hosszuhegy, Csorvás (I. Joo), Keszthely: Vadaskert, Köszeg: Kálvária, Magyarkut, Nagymaros: Hegyestetö, Nográdveröce (S. Endrödi), Orosháza, Szentendre, Telkibánya; on *Q. pubescens* Willd. (I), Leányfalu, Pécs: Misinatetö, Sima; often heavy infestations on *Q. robur* L., Erdöbénye (A. Terpo), Gézaháza, Monori-erdő, Nagykállo, Nyiregyháza: Sosto (A. Terpo), Szarvas: Arboretum, Veszprém; on *Q. robur* f. *concordia* (Kirchn.) K. Koch (I), Zirc in park; on *Q. rubra* L. (II), Szarvas: Arboretum; on *Quercus* sp. (I), Solymár.

Parasites.—Encyrtidae: *Anabrolepis zetterstedti* (Westw.), *Metaphycus insidiosus* (Merc.), *M. parvus* (Merc.), *Microterys sylvius* (Dalm.) (5, 10).

***Pulvinaria artemisiae** Sign. On roots and underground portion of stems of *Artemisia* sp. (I), Budapest: Sashegy, May 1956.

Pulvinaria betulae (L.). Isolated infestations were found unless otherwise noted. On twigs and often on the new bark. On *Acer platanoides* L., Budapest; on roadside trees of *A. pseudoplatanus* L., Budapest: Gellérthegy; on roadside trees of *Aesculus hippocastanum* L., Budapest: Lipotmezö (G. Balás and M. K.), Keszthely, Pécs; on *Alnus glutinosa* (L.) Gaertn., Zalaszentgrot; several egg-laying ♀ ♀ on *Carpinus betulus* L. (fig. 9), Budapest: AAH., May 1950; on *Corylus avellana* L., Budaörs: Kamaraerdő (I. Babbnigg and I. Joo), Budapest: AAH., May 3, 1951 (G. Jenser); heavily parasitized ♀ ♀ on *Crateagus monogyna* Jacq., Budaörs: Kamaraerdő, Budapest: AAH., Pécs (G. Balás), Sima, Tatatováros kert (G. Balás and M. K.); most of the scales on *C. oxyacantha* L. were parasitized, Budaörs: Kamaraerdő; on *Euonymus europaea* L., Kámon, Zalaszentgrot in park; on *E. verrucosus* Scop., Budapest: Látohegy (G. Balás), Gönc; two ♀ ♀ on *Juglans regia* L., Pécs; one ♀ on *Populus canescens* (Ait.) Smith, Budatétény; one ♀ on *P. nigra* var. *italica* (Münchh.) Koehne, Kelebia (J. Erdös and M. K.); one ♀ on *Prunus domestica* L., Kámon; on *Pyrus communis* var. *pyraster* L., Budapest: Látohegy; two ♀ ♀ on *P. communis* var. *sativa* (DC.) DC., Budaörs: Kamaraerdő; by the base of twigs of *Ribes rubrum* L. (III), Budatétény (J. Domokos); two ♀ ♀ on *Salix alba* var. *vitellina* (L.) Stokes, Budapest (G. Balás); on *S. repens* var. *rosmarinifolia* (L.) Wim. et Grab., Ágasegyháza, May 1, 1952; on *Salix* sp., Budapest: AAH.; on a twig on *Sorbus torminalis* (L.) Crantz (III), Budapest: Farkasvölgy (G. Balás); five ♀ ♀ on *Vitis vinifera* L., Szigetcsép (J. Kurusa).

Parasites.—Aphelinidae: *Coccophagus gigas* Erdös. Tridymidae: *Eunotus merceti* Masi. Encyrtidae: *Metaphycus insidiosus* (Merc.) (3, 10).

Family DIASPIDIDAE

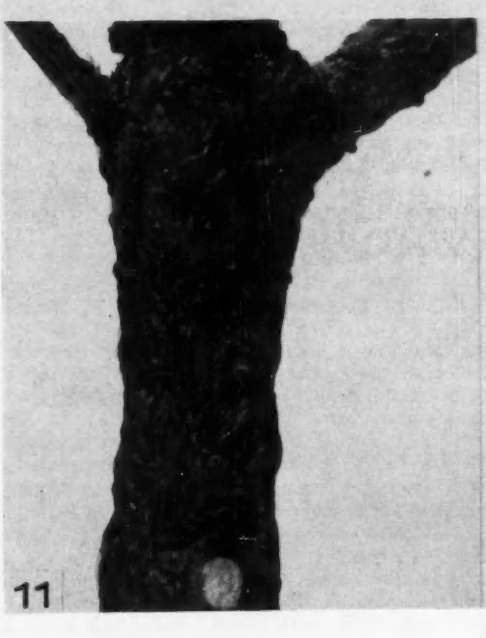
Leucaspis pini (Hartig). Heavy infestations at the base of needles of *Pinus nigra* Arn., Budapest: AAH. (fig. 10). Heavily parasitized. On

EXPLANATION OF PLATE III

FIG. 9.—*Pulvinaria betulae* (L.), females with egg sacs on *Carpinus betulus* L. FIG. 10.—*Leucaspis pini* (Hartig) on needles of *Pinus nigra* Arn. FIG. 11.—*Lepidosaphes ulmi* (L.), layered infestation on a branch of *Fraxinus excelsior* L. FIG. 12.—*Chionaspis lepineyi* Bal., male scales on a branch of *Quercus robur* L.

9

10


11

12

P. ponderosa Dougl. ex Lawson (I), Sopron in park; on *P. sylvestris* L. (I), Budapest: Hüvösvölgy (N. Tetmajer); on *P. tabuliformis* Hort. ex Carr. (III), Sopron (N. Tetmajer and M. K.).

Parasites.—Aphelinidae: *Aphytis abnormis* (How.), *Azotus pinifoliae* Merc., *Prospaltella leucaspidis* Merc. Thysanidae: *Thysanus subaeneus* (Först.). Encyrtidae: *Anthemus leucaspidis* Merc. (10).

Leucaspis pusilla Loew. On needles of *Pinus mugo* Turra (I), Sopron in park; on *P. nigra* Arn. (II), Keszthely: Vadaskert, Sopron; on *P. sylvestris* L. (I), Bezeréd and Csáford in Zala, Kőszeg, Sopron (N. Tetmajer and M. K.).

Anamaspis loewi (Colvée). The most important scale on pine in Hungary. On needles of *Pinus mugo* Turra (I), Budapest: Zuglo; occasionally heavy infestations with deformation of needles on *Pinus nigra* Arn., Ágasegyháza, Bakonybél, Balatonakali (I. Benedek), Balatonszéplak, Budaörs: Kamaraerdő (G. Balás), Budapest: Kőbánya, Margitsziget, Népliget, Sashegy (G. Balás) and Zuglo, Gödöllő, Magyarovár, Nyárlőrinc (A. Csáky), Orosháza: Gyopáros, Pécs: Misinatető, Piliscsaba (V. Stubnya), Solymár, Szarvas: Arboretum, Tatabánya, Tompa: Zsiroskuti-erdő (J. Erdös and M. K.), Veszprém, Visegrád; on needles of *P. sylvestris* L. (I), Budapest: Hüvösvölgy (N. Tetmajer), Mátrafüred.

Parasites.—Aphelinidae: *Prospaltella leucaspidis* Merc. Encyrtidae: *Anthemus leucaspidis* Merc. (5, 10).

Lepidosaphes sp. Closely related to *Lepidosaphes conchyformis* (Gmel.). One of the most obvious differences is that this species always has more than three (usually five or six) pores at the anterior spiracles. *Lepidosaphes conchyformis* (Gmel.) has only one to three pores. The author will describe this species in a subsequent publication.

On trunk of *Fraxinus ornus* L. (I), Szarvas: Arboretum; on branches of *Tilia platyphyllos* f. *laciniata* (Loud.) V. Engler (I), Budapest: AAH. (G. Balás); on trunk and branches of *T. tomentosa* Moench (I), Alsotekerespuszta, Nov. 21, 1950; on trunk, branches, and twigs of *Tilia* sp. (I), Budapest: Margitsziget, Nov. 18, 1950, Gödöllő: Szabadságpark, Apr. 23, 1952 (G. Balás and M. K.), Tata, Aug. 11, 1953 (G. Balás), Tatatóvároskert, Aug. 17, 1950 (G. Balás).

Lepidosaphes conchyformis (Gmel.). On branches of *Syringa vulgaris* L. (I), Mátészalka; on twigs of *Ulmus carpinifolia* var. *Dampieri* (Wesm.) Rehd. (I), and on *U. carpinifolia* var. *Wredei* (Jühlke) Rehd. (I), Budapest: AAH. (G. Balás); occasionally medium infestations on trunk, branches, twigs, and leaves: on *U. glabra* Huds., Balatonfüred (I. Joo), Budapest: AAH. (G. Balás), Nagymaros, Tata (G. Balás), Visegrád; on *Ulmus* sp. (I), Budapest: AAH. (G. Balás and M. K.), Mátészalka, Nagytétény (G. Balás), Orosháza, Tatatóvároskert (G. Balás and M. K.).

***Lepidosaphes granati** Kor. Isolated infestations on the trunk under peeling bark. On *Crataegus crus-galli* L., and *C. monogyna* Jacq., Budapest: AAH.; on *C. oxyacantha* L., Budapest; AAH. and Kelenhegyi-ut; on *C. sorbifolia* Lange, Budapest: AAH.

Lepidosaphes newsteadi (Šulc). Isolated infestations on needles of *Pinus nigra* Arn., Gödöllő, Veszprém.

Lepidosaphes ulmi (L.). Previously only the unisexual race was known from Hungary. Dr. J. Erdös collected several winged males of this species from *Vaccinium myrtillus* L. host, which were found in North Hungary (Hegyalja: Dobozér) on July 21, 1955. The author received this material and identified them as *Lepidosaphes ulmi bisexualis* Thiem.

One of the most common scales in parks and orchards in Hungary. Isolated infestations were noted, unless indicated otherwise. On twigs of *Aesculus hippocastanum* L., Budapest: Lipotmező (G. Balás and M. K.), Keszthely; on twigs of *Betula pendula* Roth (III), Budapest: Népliget (D. Suhajda); on twigs and shoots of *Buxus sempervirens* L., Budapest: AAH., Zalaszentgrot (I. Joo) and on *B. sempervirens* f. *glauca* Hort., Budapest: AAH (G. Balás); on trunk and twigs of *Caragana arborescens* Lam. (II), Budapest: AAH. (G. Balás and M. K.); on trunk, branches, and twigs of *C. spinosa* (L.) De Candolle (IV), Budapest: AAH.; on branches and twigs of *C.* (Michx.) K. Koch., Zirc, in park; on twigs of *Cornus mas* L., Nyiregyháza (G. Jenser); occasionally heavy infestations on trunk and twigs of *C. sanguinea* L., Budaörs: Kamaraerdő, Budapest: AAH. (G. Balás), Visegrád; on branches of *Cotoneaster divaricata* Rehd. et Wils., Budapest: AAH.; on branches and twigs of *C. horizontalis* Dcne. (III), Csákvár (A. Terpo); on branches of *Cotoneaster* sp. (II), Budapest: AAH. (G. Balás); on trunk and branches of *Crateagus monogyna* Jacq., Szentendre, Visegrád, Zirc in park; on trunk of *C. oxyacantha* L., Nagymaros; on twigs of *Crataegus* sp. (III), Budapest: AAH. (G. Balás); five ♀ ♀ on a twig of *Cydonia oblonga* Mill., Ágasegyháza; on twigs of *Cytisus ratisbonensis* Schaeff., Pilisborosszentiván: Ördögtorony (G. Balás); layered infestations on trunk and branches of *Fraxinus excelsior* L. (fig. 11), Budapest: AAH. (G. Balás), Tinnye; on branches of *Juglans* sp. (IV), Budapest: AAH. (G. Balás); a few ♀ ♀ on a branch of *Ligustrum vulgare* L., Budaörs: Kamaraerdő; on twigs of *Lycium halimifolium* Mill., Budapest: Kőbánya; medium, or occasionally heavy, infestations on trunk and branches of *Malus pumila* Mill., Budapest: AAH. and Kispest (I. Nyékes and M. K.), Telkibánya, Zirc; on trunk of *M. sylvestris* (L.) Mill., Gönc, Telkibánya; on branches and twigs of *Populus alba* L. (IV), Ágasegyháza,

Nagytétény (G. Jenser); often layered infestations on trunk, branches, and twigs of *P. nigra* var. *italica* (Münchh.) Koehne, Bátorliget (G. Balás), Békásmegyer, Nagytétény, Pécs: Balokány; on branches and twigs of *Populus* sp. (III), Budapest: AAH. (G. Balás), Soroksár (I. Sümegi), Pomáz (J. Poti); one ♀ on a branch of *Prunus armeniaca* L., Budaörs: Kamaraerdö (G. Balás); medium infestation on branches of *P. domestica* L., Budapest (G. Balás), and isolated infestation at Budaörs: Kamaraerdö; on branches of *P. spinosa* L., Budaörs: Kamaraerdö; on branches of *Quercus audleyensis* Henry, Budapest: AAH. (G. Balás); on trunk of *Q. cerris* L., Ördögárok; on branches and twigs of *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy, Pereshegy in Pilisi Mtns., Radvány, Sopron (N. Tetmajer and M. K.); one ♀ on *Q. pubescens* Willd., Budapest: Hüvösvölgy; on twigs of *Q. robur* L., Budapest: Köbánya and Látohegy (G. Balás); on twigs of *Ribes aureum* Pursh. (II), Budapest: Kispest; heavy infestations on twigs of *Robinia pseudacacia* L., Budapest: Vágohid, Tihany (J. Domokos), and isolated infestation in Budapest: Népliget; on twigs of *Rosa* sp. (II), Budapest: AAH. (G. Balás); occasionally heavy infestations on branches and twigs of *Salix* sp., Balatonfenyves (J. Lehoczky), Bátorliget (G. Balás), Padány in Komárom (G. Balás), Pomáz: Köhegy, Tatabánya; on twigs of *Spiraea salicifolia* L., Budapest: AAH. (G. Balás); on twigs of *Symphoricarpus albus* (L.) Blake, Budapest: Szépvölgy (V. Martinovich); occasionally heavy infestations on branches and twigs of *Syringa vulgaris* L., Budapest: AAH. (G. Balás), Kápolna tér, Népliget and Tabán (M. Gianonne), Nagykállo, Tatabánya; on branches and twigs of *Tamarix gallica* L., Budapest: AAH. (G. Balás and M. K.) and Kispest, Tinnye; on branches of *T. tetranda* Pall., Budapest: AAH.; several larvae on leaves and heavy infestation on twigs of *Tilia* sp., Szombathely, Sept. 24, 1950; on branches of *Ulmus* sp. (II), Nyiregyháza (G. Balás); on shoots of *Vaccinium myrtillus* L., Köszeg, Sopron (N. Tetmajer and M. K.).

Parasites.—Aphelinidae: *Aphytis abnormis* (How.), *Pteroptrix maritima* Nik., *P. opaca* Erdös. Encyrtidae: *Anabrolepis zetterstedti* (Westw.), *Apterencyrtus microphagus* (Mayr), *Eusemion cornigerum* (Walk.); *Habrolepis dalmani* Westw. (3, 5, 10, 11, 14).

Chionaspis lepineyi Bal. Several males and females in small areas. On branches and twigs of *Quercus cerris* L., Budaörs: Kamaraerdö, Holdvilágárok, Nográdveröce (S. Endrödi), Pomáz: Köhegy; on trunk and branches of *Q. petraea* (Matt.) L. ex Liebl., Abasár (A. Terpo), Budapest: Hüvösvölgy; on branches and twigs of *Q. pubescens* Willd., Budapest: Hüvösvölgy (N. Tetmajer), Csobánka: Hosszuhegy, Pécs: Misinatetö, Aug. 12, 1953 (winged males also), Szentendre, Aug. 4, 1953 (winged males also); on trunk of *Q. robur* L. (III) (fig. 12), Veszprém; heavy infestation with male scales also on trunk and branches of *Quercus* sp., Fertöd, Aug. 7, 1951 (S. Kaszonyi), Keszthely (I)

Parasites.—Aphelinidae: *Aspidiotiphagus citrinus* (Craw), *Coccophagoides similis* Masi. Thysanidae: *Thysanus subaeneus* (Först.) (10).

Chionaspis salicis (L.). On twigs of *Acer campestre* L. (I), Zirc in park; on branches and twigs of *Alnus glutinosa* (L.) Gaertn. (I), Dabas, July 12, 1955 (A. Terpo), Martonvásár in park, June 29, 1955; on branches and twigs of *Cornus sanguinea* L. (III) (fig. 13), Budaörs (G. Balás), Budapest: Szépvölgy (G. Balás); on trunk and twigs of *Fraxinus excelsior* L. (III), Budapest: Margitsziget (G. Balás), Dabas, June 9, 1956, Nagyhideghegy; on trunk of *F. ornus* L. (III), Magyarovár; on branches of *F. pennsylvanica* Marsh. (III), Dabas (A. Terpo); on trunk and branches of *Populus alba* L. (I), Budapest: Zoo, Kelebia (J. Erdös and M. K.), Nagytétény (G. Balás); on trunk and branches of *Populus* sp. (I), Nagytétény, Szeged in park (G. Balás and I. Joo); on branches and twigs of *Salix alba* L. (I), Tatatovároskert (G. Balás and M. K.); on branches of *S. caprea* L. (I), Gönc; on branches and twigs of *Salix* sp. (III), Padány in Komárom (G. Balás), Tatatovároskert (G. Balás and M. K.).

Parasite.—Encyrtidae: *Kosztarabia chionaspidis* Erdös (4).

Unaspis euonymi (Comst.). Important pest in Hungary. Often layered infestations on branches, twigs, leaves, and fruits of *Euonymus europaea* L. (fig. 14), Budapest: AAH. (B. Varga), Kerepesitemetö (G. Balás), and Tabán (M. Gianonne, V. Martinovich, and B. Szabo); on twigs and leaves of *E. japonica* Thunbg. (III), Budapest: Botanical Garden (G. Balás) and Kerepesi-temetö (I. Joo), Pécs; on twigs and leaves of *E. latifolia* (L.) Mill. (III), Budapest: AAH. (G. Balás); on twigs and leaves of *E. fortunei* var. *radicans* (Miq.) Rehd. (III), Budapest: Botanical Garden (G. Balás); on branches and twigs of *E. verrucosus* Scop. (IV), Budapest: Sashegy, Aug. 22, 1955. Several winged males were collected from this material.

Parasite.—Aphelinidae: *Aspidiotiphagus citrinus* (Craw) (10).

Aulacaspis rosae (Bouché). Important pest. Occasionally heavy infestations on branches and twigs of *Rosa canina* L., Bicske (L. Gaál), Budakeszi (K. Kemény), Kerekes Mtn. in Pilisi Mtns., Tihany; often heavy infestations on branches and twigs of *Rosa* sp., Balatonföldvár, Balatonfüred (I. Joo), Békásmegyer, Bezeréd, Bögellö in Komárom (G. Balás), Budakeszi (K. Kemény), Budapest: Gellérthegy, Látohegy and Margitsziget, Csáford, Debrecen (G. Balás), Eger, Esztergom (E. Horváth), Herény, Kecskemét (N. Kovács), Keszthely, Magyarovár, Mátészalka, Nagykállo, Nagymaros, Nyiregyháza, Padány (G. Balás), Pápa, Pécs, Sima, Sopron, Zala-

szentgrot in park and cemetery; on twigs of *Rubus caesius* L. (I) (caused reddish discoloration on green shoots), Nagytétény, Szatmárökörito (G. Balás), Zalakoppány; heavy infestation on twigs of *Rubus* sp., Békés (S. Kiss) and isolated infestations in Budaörs: Kamaraerdö (G. Balás) and Máriahegy in Somogy (A. Károlyi).

Parasites.—Aphelinidae: *Aspidiotiphagus citrinus* (Craw). Encyrtidae: *Anabrolepis mayri* (Rschk.), *Aphytis proproclia* (Walk.), *Apterencyrtus microphagus* (Mayr), *Arrhenophagus chionaspidis* Aur. (10).

Pseudaulacaspis pentagona (Targ.). A pest in South Hungary. Always heavily parasitized. On branches and twigs of *Morus alba* L. (III), Máriagyüd (M. Huba), Pécs: Balokány (I. Balogh and M. K.).

Parasite.—Aphelinidae: *Prospaltella berlesei* (How.) (1).

Carulaspis visci (Schr.). On leaves of *Chamaecyparis Lawsoniana* (Murr.) Parl., Köszeg, Sopron; on stem and leaves of *C. thyoides* f. *ericoides* (Carr.) Rehd., Sopron; on leaves of *Juniperus chinensis* L., Budapest: AAH., Tatatóváros kert (G. Balás and M. K.); on leaves on *J. communis* L., Budapest: Hüvösvölgy (N. Tetmajer), Csáford, Kámon, Köszeg (T. Pomogyi), Magyarkut, Nagymaros, Orosháza: Gyopáros (I. Joo), Sopron, Sümeg (Olasz), Szeged: Botanical Garden; on leaves of *J. sabina* L., Budapest: AAH. (G. Balás); on leaves and fruits of *J. sabina* var. *tamariscifolia* Ait., Sopron; on leaves and fruits of *J. virginiana* L., Sopron, Szarvas: Arboretum (N. Tetmajer and M. K.), Visegrád; on leaves of *Thuja occidentalis* L., Keszthely, Köszeg, Zalaegerszeg.

A common scale on the leaves and fruits of *Thuja orientalis* L., although damage was not noted. Alsotekerespuszta, Balatonfüred (I. Joo), Budapest: Gellérthegy, Cégénydányád (I. Joo), Eger, Hajduhadháza (I. Joo), Kecskemét, Komárom (G. Balás), Köszeg, Magyarovár, Orosháza, Pápa, Pécs, Sopron. Only isolated infestations were noted on the other hosts.

Epidiaspis leperii (Sign.). Small, local infestations on the trunk of *Aesculus hippocastanum* L., Balatonföldvár, Budapest: Margitsziget, Pécs, Visegrád; on branches of *Cotoneaster acutifolia* Turcz. (II) and *Cotoneaster* sp. (III), Budapest: AAH. (G. Balás and M. K.); infested spots on the branches of *Crataegus monogyna* Jacq., which caused pits, Szigetszentmiklos (Gy. Toth); on the trunk of *C. pentagyna* W. et K. (II), Budapest: AAH.; on the trunk and branches of *Malus pumila* Mill. (III), Budaörs: Kamaraerdö, Budapest: Testvérhegy, Ráckeve, Sopron, Telkibánya, Tihany; on the trunk of *M. sylvestris* (L.) Mill. (I), Telkibánya; on the trunk and branches of *Malus* sp. (I), Budapest: AAH. (G. Balás), Szarvas: Arboretum; often heavy infestations on trunk and branches of *Prunus domestica* L., which often caused pits. Alsotekerespuszta, Budaörs: Kamaraerdö, Budapest: AAH. (G, Balás and M. K.), Kelenhegyi-ut and Szépvölgy, Dánszentmiklos, Kámon, Nagymaros, Pomáz, Tekenye in Zala, Visegrád; on trunk and branches of *P. insititia* L. (I), Sopron; on branches of *P. spinosa* L. (II), Budapest: Sashegy; on branches and twigs of *Pyrus elaeagrifolia* Pall. (II), Sopron; on branches and twigs of *P. nivalis* Jacq. (II), Szentendre; often heavy infestations on trunk and branches of *P. communis* var. *pyraster* L., Budapest: Látohegy, Cégénydányád (I. Joo), Fánivölgy, Lomhegy in Pilisi Mtns., Pécs, Sima, Sopron, Telkibánya; on trunk and branches of *P. salicifolia* Pall. (I), Budapest: AAH., Sopron; on trunk, branches and twigs of *P. communis* var. *sativa* (DC.) DC. (III), (important scale on this host and caused pits at the site of infestation), Balatonfenyves (B. Skublics), Bezeréd, Bicske (E. Peterdy), Budafok (I. Kanyo), Budapest: Gellérthegy, Jász-utca (I. Tohai), Sashegy and Tarcali-utca (G. Szelényi), Dánszentmiklos, Felsömindszent (J. Ceglédi), Fenékpuszta, Kony (M. Máté), Köszeg (A. Terpo), Maglod (A. Boros), Monor (M. Dömötör), Nagykállo, Nagymaros, Solymár (J. Dévényi), Örszentmiklos (G. Jenser), Pomáz: Kiscsikovár, Sopron, Tekenye, Tihany, Zirc; on branches of *Sorbus aucuparia* L. (I), Budaörs: Kamaraerdö (G. Balás); on branches of *S. domestica* L. (I), Budapest: AAH. (G. Balás).

Dynaspidiotus abietis (Schr.). On needles only. Often on *Picea alba* Mill., Bakonybél in park, Balatonföldvár, Csáford, Fertöd, Gödöllö, Gönc, Keszthely, Magyarovár, Orosháza: Gyopáros, Pécs, Pomáz; on *P. pungens* f. *glauca* (Reg.) Beiss. (III), Pomáz; on *P. sitchensis* (Bong.) Carr. (I), Sopron in park.

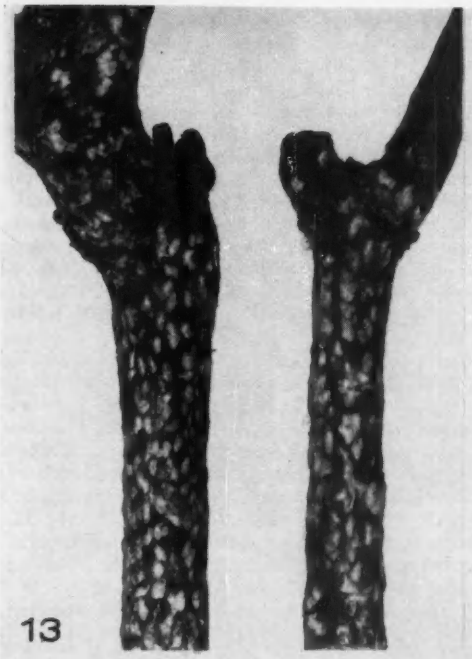
Parasites.—Aphelinidae: *Aphytis abnormis* (How.), *Prospaltella aspidioticola* Merc. (10).

***Chortinaspis subterraneus** (Lndgr.). A few ♀ ♀ on parts of underground stems and on the rhizomes of *Agropyron repens* (L.) Beauv., Budapest (G. Balás).

Quadraspidiotus gigas (Thiem and Gern.). On branches of *Populus alba* L. (I), Budapest: AAH. (G. Balás), Nagykállo; on twigs of *P. berolinensis* Dipp. (IV), Budapest: Botanical Garden (G. Balás); on branches and twigs of *P. nigra* L. (IV),

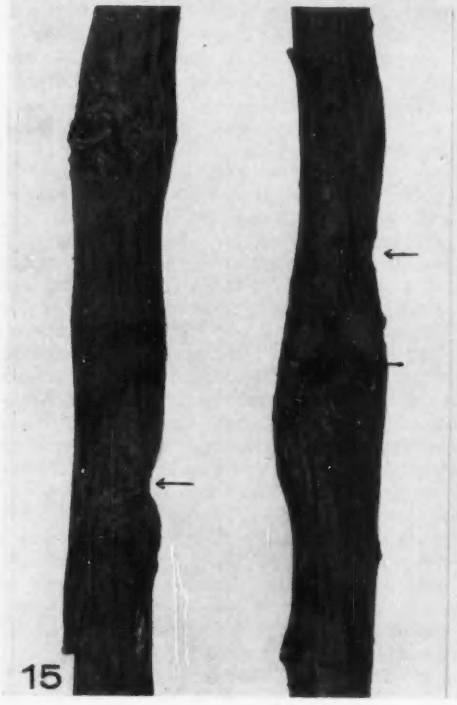
EXPLANATION OF PLATE IV

FIG. 13.—*Chionaspis salicis* (L.) on twigs of *Cornus sanguinea* L. FIG. 14.—*Unaspis euonymi* (Comst.), infestation on twigs, leaves, and fruits of *Euonymus europaea* L. FIG. 15.—*Quadraspidiotus gigas* (Thiem and Gern.) causing pits in twigs of *Populus nigra* var. *italica* (Münchh.) Koehne. FIG. 16.—*Quadraspidiotus perniciosus* (Comst.), male scales on leaves of *Prunus domestica* L.



13

14



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16

Szolnok: cemetery and Tata (G. Balás); often layered infestations on branches and twigs of *P. nigra* var. *italica* (Münchh.) Koehne. Important scale on this host, causing pits (fig. 15) in the infested branches and twigs. Békásmegyer, Budapest: Buda and Köbánya, Fényeslitke (A. Terpo), Nyárlörinc, Pécs: Balokány, Tinnye; on trunk of *P. trichocarpa* Torrey et Gray ex Hook. (I), Sopron; on branches and twigs of *Populus* sp. (I), Budapest: AAH. (G. Balás and M. K.), Nagytétény; on branches and twigs of *Salix alba* L. (II), Tatatóváraskert (G. Balás and M. K.), Zalaszentgrot; on branches and twigs of *Salix* sp. (II), Budaörs: Kamaraerdö (G. Balás), Budapest: AAH., Tatabánya.

Parasites.—Aphelinidae: *Aspidiotiphagus citrinus* (Craw), *Azotus matritensis* Merc., *Pteroptrix dimidiata* Westw., *P. maritima* Nik. (10).

***Quadraspidiotus lenticularis** (Lndgr.). On trunk and branches of *Quercus petraea* (Matt.) L. ex Liebl. (I), Budapest: Hüvösvölgy; on trunk of *Quercus* sp. (I), most on the growing portion of the bark, Pomáz.

***Quadraspidiotus marani** Zahr. This scale is important in Hungarian orchards. In the past it was identified as *Q. pyri* (Licht.). On branches and twigs of *Crataegus oxyacantha* L. (III), Magyarovár; on trunk of *Fraxinus excelsior* L. (I), Magyarovár; on trunk and branches of *F. ornus* L. (I), Monori-erdö; on trunk of *Prunus avium* L. (III), Nagytétény, (Zs. Tatár); on trunk of *P. domestica* L. (I), Szilvásvárad; on branches of *P. spinosa* L. (II), Budapest: Sashegy; on trunk and branches of *Prunus* sp. (III), Nagykevély; on branches of *Pyrus communis* var. *sativa* (DC.) DC. (II), Budafok (I. Kanyo).

Quadraspidiotus ostreaeformis (Curt.). Common and damaging in Hungary. Isolated infestation unless noted otherwise. On branches and twigs of *Acer campestre* L., Budapest: AAH. (G. Balás), Magyarovár and medium infestation Zebegény: Törökmezö; on the healing parts of the damaged trunk of *A. platanoides* L., Budapest; in small areas, particularly under the loose bark of trunk of *Aesculus hippocastanum* L., Alsotekerespuszta, Budaörs: Kamaraerdö, Budapest: Hüvösvölgy, Margitsziget, and Köbánya, Keszthely, Kiskunhalas, Köszeg, Magyarovár; on trunk of *Alnus glutinosa* (L.) Gaertn. (II), Szentendre, Zalaszentgrot; on the healing parts of the damaged trunk of *Betula pendula* Roth, Budapest: AAH. and Köbánya, Csáford; on trunk and twigs of *Caragana arborescens* Lam., Budapest: AAH. (G. Balás and M. K.), Fertöd, Gödöllö; on trunk of *Carpinus betulus* L., Budapest: Hüvösvölgy, Csobánka: Hosszuhegy, Sima, Visegrád: Lepence-völgy, Zalaszentgrot; on trunk and branches of *Catalpa bignonioides* Walt., Budapest: Népliget; on trunk of *Cladrastis lutea* (Michx.) K. Koch., Budapest: Margitsziget; on branches and twigs of *Cornus sanguinea* L., Balatonfüred. Budapest: AAH. (G. Balás and M. K.); on trunk of *Corylus avellana* L., Magyarovár and medium infestation Budaörs: Kamaraerdö; on trunk of *Crateagus monogyna* Jacq.- Budapest: AAH., Sima, and heavy infestation Budaörs: Kamaraerdö; on branches of *C. orientalis* Pall., Szarvas: Arboretum; in small areas, particularly under the loose bark of the trunk, of *C. oxyacantha* L., Budapest: Kelenhegyi-ut; on trunk and branches of *Crataegus* sp., Nagymaros, Solymár; on twigs of *Euonymus europaea* L., Budaörs: Kamaraerdö; on twigs of *E. verrucosus* Scop., Budaörs: Kamaraerdö (G. Balás); on trunk and twigs of *Fraxinus excelsior* L., Budapest: Margitsziget, and heavy infestation Budapest: Szabadsághegy; on trunk and branches of *Fraxinus* sp. (II), Budapest: AAH. (G. Balás), Hatvan; two ♀ ♀ on a twig of *Juglans regia* L., Visegrád; on twigs of *Ligustrum vulgare* L., Budaörs: Kamaraerdö, Budapest: AAH. (G. Balás and M. K.); on trunk of *Malus pumila* Mill. (II), Telkibánya, Zirc; on trunk of *M. sylvestris* (L.) Mill., Sima, Telkibánya; on trunk and branches of *Prunus avium* L. (III), Budapest: AAH. and Széchenyi Mtn., Visegrád; on branches of *P. cerasifera* var. *atropurpurea* (Jaeg.) Rehd. Badacsonyörs, Zirc; on trunk of *P. cerasus* L. (II), Rákospalota (Z. Baráth), Soroksár; on trunk of *P. domestica* L., Aranyosfürdö, Szilvásvárad, Tatabánya; on trunk and branches of *P. mahaleb* L. (II), Nagymaros, Solymár; on branches of *P. spinosa* L. (III), Budaörs: Kamaraerdö; on twigs of *Prunus* sp., Budapest: AAH. (I. Joo); on trunk and branches of *Pyrus communis* var. *pyraster* L., Telkibánya; on trunk and branches of *Rhamnus cathartica* L. (III), Budaörs: Kamaraerdö, Budapest: AAH. (G. Balás); on twigs of *Ribes aureum* Pursh. (III), Mátészalka in park; on twigs of *R. grossularia* L., Soroksár; on *R. nigrum* L. (II), Budapest: AAH. (G. Balás); on the healing parts of the damaged trunk of *Sorbus torminalis* (L.) Crantz, Pomáz; often medium infestations on trunk, branches, and twigs of *Syringa vulgaris* L., Budapest: AAH. (G. Balás), Budagyöngye (D. Suhajda) and Kispest, Jászberény, Magyarovár, Monori-erdö, Szarvas (G. Balás), Tatabánya; occasionally medium infestations on trunk and branches of *Tilia cordata* Mill., Békéscsaba (I, Joo), Dobogokö, Hatvan, Holdvilágárok, Nagymaros, Pécs: Balokány, Szombathely, Zirc in park; on trunk of *T. platiphyllos* Scop., and *T. platiphyllos* f. *laciniata* (Loud.) V. Engler, Budapest: AAH; occasionally medium infestations on trunk, branches and twigs of *Tilia* sp., Békéscsaba (G. Balás), Budaörs (G. Balás), Dánszentmiklos, Sopron, Visegrád; on branches and twigs of *Viburnum opulus* L. (II), Csáford.

Parasites.—Aphelinidae: *Aphytis bovelli* (Mal.), *Azotus matritensis* Merc., *A. pinifoliae* Merc., *Coccophagoides similis* (Masi), *Pteroptrix maritima* Nik. (10).

Quadraspidiotus perniciosus (Comst.). The

most important scale in Hungary. Isolated infestations unless otherwise noted. On branches and twigs of *Betula pendula* Roth (III), Pécs: Balokány, Aug. 13, 1953; on the healing parts of the damaged trunk of *Broussonetia papyrifera* (L.) L'Hérit, Budapest: Zuglo; on *Chaenomeles japonica* (Thunb.) Lindl., Szeged (G. Balás); on branches and twigs of *C. japonica* var. *cardinalis* Carr. (IV), Budapest: AAH.; on twigs, leaves, and fruits of *Cotoneaster* sp. (III), Budapest: AAH. (G. Balás and I. Joo); on *Crataegus monogyna* Jacq., Nagykállo, heavy infestation at Nyiregyháza (G. Jenser), Türje, Zalaszentgrot; on branches and twigs of *C. oxyacantha* L., Balatonszéplak, Eger, Tökol (G. Jenser), layered infestation in Budaörs: Kamaraerdö; on branches of *Crateagus* sp. (III), Budaörs: Csiki Mtn. (Z. Baráth and A. Terpo), Szeged (G. Balás); on trunk of *Cydonia oblonga* Mill., Dánszentmiklos, Tekenye; on twigs and leaf petioles of *Juglans regia* L. (II), Tekenye; on branches and twigs of *Maclura pomifera* (Raf.) Schneider (*iv*), Keszthely: on trunk and branches of *Malus baccata* var. *mandshurica* (Maxim.) Schneid. (II), Sopron; on branches of *M. baccata* sp., Kámon; often layered infestations on trunk, branches and twigs of *M. pumila* Mill., Alpár (Sz. Kalmár), Boldva in Borsod, Budapest: Szépvölgy, Dánszentmiklos, Lajosmizse (Gy. Bene), Méhtelek (I, Horváth), Nagykállo, Tihany, Tiszacsécse, Visegrád, Zalaszentgrot (V. Martinovich); on trunk and branches of *M. pumila* var. *Niedzwetzkyana* (Dieck.) Schneid. (II), Kámon; on trunk and branches of *M. sylvestris* (L.) Mill. (II), Bátorliget, Sopron; on trunk and branches of *Malus* sp. (III), Kámon, Mezöcsokonya (L. Jezerniczky), Pécs, Szarvas: Arboretum; on trunk, branches, twigs and fruits of *Mespilus germanica* L. (III), Kámon, Leányfalu, Nagymaros, Pomáz, Szentendre (S. Kaszonyi); on trunk and branches of *Prunus amygdalus* Batsch., Nagymaros, Szentendre; on trunk and branches of *P. armeniaca* L., Csáford, Nyárlörinc, Visegrád, layered infestation at Monori-erdö; occasionally heavy infestations on trunk, branches, twigs and leaves of *P. avium* L., Budapest: Gellérthegy, Dánszentmiklos, Debrecen, Lajosmizse (Gy. Bene), Szombathely, Tekenye, Zalaszentgrot; occasionally layered infestations on branches and twigs of *P. cerasifera* Ehrh., Békásmegyer, Budapest: Margitsziget, Kámon, Tiszalök; on branches of *P. cerasifera* var. *atropurpurea* (Jaeg.) Rehd. (III), Pécs, Szarvas: Arboretum, Zalaszentgrát in park; often heavy infestations on trunk, branches and twigs of *P. domestica* L., Cégénydányád, Aug. 20, 1955 (I. Joo; several males on leaves, fig. 16), Herény, Lajosmizse (Gy. Bene), Nagykállo, Nyiregyháza: Sosto (A. Terpo); on twigs and leaves of *P. laurocerasus* L., Pécs: Balokány; on trunk and branches of *P. mahaleb* L. (III), Tiszacsécse; on trunk, branches and twigs of *P. padus* L., Magyarovár, Szombathely; on branches and twigs of *P. persica* (L.) Batsch. (II), Csáford, Nagykállo, Nyiregyháza, Tura, Zalaszentgrot; on trunk and branches of *P. serotina* Ehrh., and *P. serrulata* Lindl., Sopron in park; often heavy infestations on branches and twigs of *P. spinosa* L., Fánivölgy, Keszthely, Pomáz: Kiscsikovár, Tekenye, Tihany, Türje, Zalakoppány; on trunk and branches of *Pyrus communis* var. *pyraster* L. (III), Kámon, Zalaszentgrot; often layered infestations on trunk, branches, twigs, fruits, and occasionally males were found on leaves, of *P. communis* var. *sativa* (DC.) DC., Besenyszög, Fertöd (L. Szénási), Nagykállo, Porva (K. Ambrozi), Szentendre, Szombathely, Zalaszentgrot; on twigs of *Ribes aureum* Pursh. (III), Zalakoppány; often layered infestations on twigs of *R. rubrum* L. (damaging scale on this host.) Budaörs: Kamaraerdö (G. Balás), Budapest: AAH., Cegléd (H. Szikora), Kámon, Lajosmizse (Gy. Bene), Méhtelek (I. Horváth), Szikra (L. Tohai), Tekenye; on branches of *Rosa canina* L., Budaörs: Kamaraerdö; on branches and twigs of *Rosa* sp., Békásmegyer, Nagymaros, Zalaszentgrot; on branches and twigs of *Salix repens* var. *rosmarinifolia* (L.) Wim. et Grab. (II), Kelebia, Sept. 9, 1955; occasionally heavy infestations on branches and twigs of *Salix* sp., Békéscsaba (G. Balás), Csáford, Debrecen, Nagykállo, Zalaszentgrot in park; on branches and twigs of *Sorbus aucuparia* L. (III), Herény, Kámon; on branches of *S. aucuparia* var. *rossica* Späth. ex Koehne, Budaörs: Kamaraerdö (G. Balás); on branches of *S. domestica* L. (II), Pomáz: Kiscsikovár; on branches and twigs of *Syringa vulgaris* L., Bicske, Aug. 1953 (I. Léber—several males on the leaves); on trunk of *Tilia platyphyllos* Scop., Zalaszentgrot; on branches and twigs of *Ulmus procera* f. *Vanhouttei* (Schelle) Rehd., Budapest: Népliget; on branches and twigs of *Ulmus* sp. (III), Magyarovár; medium infestation on the cultures of *Vitis vinifera* L. growing on arbors, Besenyszög, on leaves at Monori-erdö, Oct. 11, 1950.

Parasite.—Aphelinidae: *Aphytis proclia* (Walk.) (10, 15, 17).

Quadraspidiotus pyri (Licht.). On branches of *Fraxinus excelsior* L. (I), Köszeg (A. Terpo); two ♀ ♀ on a branch of *Prunus domestica* L., Herény; on trunk and branches of *Prunus* sp. (III), Nagykevély.

***Quadraspidiotus šulci** Bal. On twigs near the ground on *Cytisus austriacus* L. (I), Budapest: Sashegy (G. Balás); on the base of twigs of *C. ratisbonensis* Schaeff. (III), Budapest: Hüvösvölgy (G. Balás) and on *Cytisus* sp. (III), Budapest: Sashegy; on the twigs which are located near the surface of the ground on *Genista tinctoria* var. *virgata* (Willd.) Koch (I), Budaörs: Kamaraerdö (G. Balás).

***Quadraspidiotus zonatus** (Frauenf.). On trunk, branches, and twigs of *Quercus petraea*

(Matt.) L. ex Liebl. (I), Budapest: Hüvösvölgy and Margitsziget (G. Balás), Köszeg, Magyarkut, Nagymaros: Hegyestetö, Pereshegy; occasionally heavy infestations on branches and twigs of *Q. robur* L., Békéscsaba (G. Balás and I. Joo), Budapest: Kőbánya and Margitsziget, Magyaróvár, Szarvas: Arboretum.

Diaspidiotus alni (March.). The most frequent scale on alder in Hungary. On trunk and branches of *Alnus glutinosa* (L.) Gaertn., Aranyosfürdö, Köszeg, Martonvásár in park, Sopron; on trunks of *Carpinus betulus* L. (II), in Pilisi Mtns.: Kétbükkfanyereg, Lajos-forrás, and Lomhegy; isolated infestation on trunk of *Fagus sylvatica* L., Budapest: Széchenyi Mtn., heavy infestations at Kétbükkfanyereg and Lomhegy.

Parasite.—Aphelinidae: *Pteroptrix dimidiata* Westw. (10).

***Diaspidiotus bavaricus** Lndgr. Isolated infestation on twigs of *Calluna vulgaris* (L.) Hull, Köszeg.

Diaspidiotus hungaricus Koszta. Isolated infestations on trunk and branches of *Quercus petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy, June 7 and July 15, 1955.

Parasites.—Aphelinidae: *Aphytis bovelli* (Mal.), *Azotus pinifoliae* Merc., *Coccophagoides similis* (Masi), *Pteroptrix dimidiata* Westw. (10).

Diaspidiotus wünni (Lndgr.). On trunk, branches, and twigs of *Quercus cerris* L. (I), Budaörs: Kamaraerdö, Budapest: Hüvösvölgy, and Látohegy, Nagymaros: Fábri-pihenö; occasionally medium infestations on trunk, branches and twigs of *Q. petraea* (Matt.) L. ex Liebl., Budapest: Hüvösvölgy, Csobánka: Hosszuhegy, Nagykevély; on branches of *Q. petraea* f. *laciniata* (Lam.) Schwarz (I), Budapest: AAH. (G. Balás); on trunk and branches of *Q. robur* L. (I), Szarvas: Arboretum, Veszprém; on the healing parts of the damaged trunk of *Quercus* sp. (I), Pomáz, Solymár.

Parasite.—Aphelinidae: *Aspidiotiphagus citrinus* (Craw) (10).

Targionia vitis (Sign.). On trunk and branches of *Quercus cerris* L. (II), Budapest: Zugliget, Nagymaros; on trunk and branches of *Q. petraea* (Matt.) L. ex Liebl. (I), Budapest: Hüvösvölgy, and on *Q. robur* L., Tompa: Zsiroskuti-erdö (J. Erdös and M. K.).

Parasites.—Aphelinidae: *Aphytis abnormis* (How.). Eulophidae: *Chrysocharidia fimbriata* Erdös. Encyrtidae: *Habrolepis pascuorum* Merc., *Ooencyrtus azureus* (Merc.) (5, 10).

LIST OF HOST PLANTS AND SCALES

Acer campestre L.: Acanthococcus aceris, Chionaspis salicis, Quadraspidiotus ostreaeformis.

Acer negundo L.: Eulecanium corni.

Acer negundo var. *odessanum* H. Rothe: Eulecanium corni.

Acer platanoides L.: Polystomophora ostiaplurima, Acanthococcus aceris, Pulvinaria betulae, Quadraspidiotus ostreaeformis.

Acer pseudo-platanus L.: Polystomophora ostiaplurima, Eulecanium corni, E. coryli, Pulvinaria betulae.

Acer saccharinum L.: Eulecanium coryli.

Achillae millefolium L.: Orthezia urticae, Asterolecanium arabidis.

Aesculus hippocastanum L.: Polystomophora ostiaplurima, Eulecanium corni, E. coryli, Pulvinaria betulae, Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus ostreaeformis.

Aesculus pavia L.: Eulecanium corni.

Agropyron intermedium (Host.) Beauv.: Rhizococcus obscurus.

Agropyron repens (L.) Beauv.: Eriopeltis festucae, Chortinaspis subterraneus.

Alnus glutinosa (L.) Gaertn.: Pulvinaria betulae, Chionaspis salicis, Quadraspidiotus ostreaeformis, Diaspidiotus alni.

Amorpha fruticosa L.: Eulecanium corni.

Anthemis tinctoria L.: Orthezia urticae.

Artemisia campestris L.: Orthezia urticae.

Artemisia sp.: Pulvinaria artemisiae.

Berberis vulgaris L.: Eulecanium persicae.

Betula pendula Roth: Lepidosaphes ulmi, Quadraspidotus ostreaeformis, Q. perniciosus.

Thuja orientalis L.: Carulaspis visci.

Broussonetia papyrifera (L.) L'Hérit: Eulecanium corni, Quadraspidiotus perniciosus.

Buxus sempervirens L.: Eulecanium corni, Lepidosaphes ulmi.

Buxus sempervirens f. *glauca* Hort.: Lepidosaphes ulmi.

Calluna vulgaris (L.) Hull: Eulecanium franconicum, Diaspidiotus bavaricus.

Campsis radicans (L.) Seem.: Eulecanium corni.

Caragana arborescens Lam.: Eulecanium corni, Lepidosaphes ulmi, Quadraspidiotus ostreaeformis.

Caragana spinosa (L.) De Candolle: Lepidosaphes ulmi.

Cardaminopsis arenosa (L.) Hayek: Orthezia urticae.

Carpinus betulus L.: Eulecanium corni, Pulvinaria betulae, Quadraspidiotus ostreaeformis, Diaspidiotus alni.

Castanea sativa Mill.: Eulecanium rufulum.

Catalpa bignonioides Walt.: Quadraspidiotus ostreaeformis.

Celtis australis L.: Eulecanium corni.

Celtis occidentalis L.: Eulecanium corni.

Cercidiphyllum japonicum S. et Z.: Eulecanium corni.

Cercis siliquastrum L.: Eulecanium corni.

Chaenomeles japonica (Thunb.) Lindl.: Quadraspidiotus perniciosus.

Chaenomeles japonica var. *cardinalis* Carr.: Quadraspidiotus perniciosus.

Chamaecyparis Lawsoniana (Murr.) Parl.: Carulaspis visci.

Chamaecyparis thyoides f. *ericoides* (Carr.) Rehd.: Carulaspis visci.

Cladrastis lutea (Michx.) K. Koch.: Lepidosaphes ulmi, Quadraspidiotus ostreaeformis.

Clematis vitalba L.: Eulecanium corni.

Colutea arborescens L.: Eulecanium corni.

Cornus mas L.: Eulecanium corni, Lepidosaphes ulmi.

Cornus sanguinea L.: Eulecanium corni, E. coryli, Lepidosaphes ulmi, Chionaspis salicis, Quadraspidiotus ostreaeformis.

Corylus avellana L.: Eulecanium corni, E. coryli, E. rufulum, Pulvinaria betulae, Quadraspidiotus ostreaeformis.

Cotoneaster acutifolia Turcz.: Eulecanium corni, Epidiaspis leperii.

Cotoneaster divaricata Rehd. et Wils.: Lepidosaphes ulmi.

Cotoneaster horizontalis Dcne: Lepidosaphes ulmi.

Cotoneaster sp.: Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus perniciosus.

Crataegus crus-galli L.: Lepidosaphes granati.

Crataegus monogyna Jacq.: Eulecanium bituberculatum, E. corni, E. coryli, Pulvinaria betulae, Lepidosaphes granati, L. ulmi, Epidiaspis leperii, Quadraspidiotus ostreaeformis, Q. perniciosus.

Crataegus orientalis Pall.: Eulecanium corni, Quadraspidiotus ostreaeformis.

Crataegus oxyacantha L.: Eulecanium bituberculatum, E. corni, E. coryli, Pulvinaria betulae, Lepidosaphes granati, L. ulmi, Quadraspidiotus mařani, Q. ostreaeformis, Q. perniciosus.

Crataegus pentagyna W. et K.: Epidiaspis leperii.

Crataegus sorbifolia Lange: Lepidosaphes granati.

Crataegus sp.: Eulecanium bituberculatum, E. corni, Lepidosaphes ulmi, Quadraspidiotus ostreaeformis, Q. perniciosus.

Cudrania tricuspidata (Carr.) Bureau: Eulecanium corni.

Cydonia oblonga Mill.: Eulecanium corni, Lepidosaphes ulmi, Quadraspidiotus perniciosus.

Cytisus austriacus L.: Quadraspidiotus šulci.

Cytisus ratisbonensis Schaeff.: Lepidosaphes ulmi, Quadraspidiotus šulci.

Cytisus sp.: Quadraspidiotus šulci.

Dorycnium suffruticosum var. *sericeum* (Neilr.) Beck: Orthezia urticae.

Elaeagnus angustifolia L.: Eulecanium corni, E. rufulum.

Euonymus europaea L.: Pulvinaria betulae, Unaspis euonymi, Quadraspidiotus ostreaeformis.

Euonymus japonica Thunbg. Unaspis euonymi.

Euonymus latifolia (L.) Mill.: Unaspis euonymi.

Euonymus fortunei var. *radicans* (Miq.) Rehd.: Unaspis euonymi.

Euonymus verrucosus Scop.: Pulvinaria betulae, Unaspis euonymi, Quadraspidiotus ostreaeformis.

Euphorbia cyparissias L.: Orthezia urticae.

Fagus sylvatica L.: Cryptococcus fagisuga, Diaspidiotus alni.

Fagus sylvatica f. *atropunicea* (West.) Domin: Cryptococcus fagisuga.

Filipendula hexapetala Gilib.: Orthezia urticae.

Fraxinus excelsior L.: Pseudochermes fraxini, Eulecanium corni, Lepidosaphes ulmi, Chionaspis salicis, Quadraspidiotus mařani, Q. ostreaeformis, Q. pyri.

Fraxinus excelsior f. *pendula* (Ait.) Schelle: Eulecanium corni.

Fraxinus ornus L.: Pseudochermes fraxini, Lepidosaphes sp., Chionaspis salicis, Quadraspidiotus mařani.

Fraxinus pennsylvanica Marsh.: Chionaspis salicis.

Fraxinus sp.: Pseudochermes fraxini, Eulecanium corni, Quadraspidiotus ostreaeformis.

Galium pumilum Murr.: Orthezia urticae.

Galium vernum L.: Orthezia urticae.

Genista tinctoria var. *virgata* (Willd.) Koch: Quadraspidiotus šulci.

Gleditschia triacanthos L.: Eulecanium corni.

Hedera helix L.: Asterolecanium arabidis.

Juglans regia L.: Eulecanium ciliatum, E. corni, Pulvinaria betulae, Quadraspidiotus ostreaeformis, Q. perniciosus.

Juglans sp.: Lepidosaphes ulmi.

Juniperus chinensis L.: Carulaspis visci.

Juniperus communis L.: Carulaspis visci.

Juniperus sabina L.: Carulaspis visci.

Juniperus sabina var. *tamariscifolia* Ait.: Carulaspis visci.

Juniperus virginiana L.: Carulaspis visci.

Ligustrum vulgare L.: Asterolecanium arabidis, Lepidosaphes ulmi, Quadraspidiotus ostreaeformis.

Lithospermum purpureocoeruleum L.: Asterolecanium arabidis.

Lonicera tatarica L.: Eulecanium corni.

Loranthus europaeus Jacq.: Eulecanium rufulum.

Lycium halimifolium Mill.: Lepidosaphes ulmi.

Maclura pomifera (Raf.) Schneider: Eulecanium corni, Quadraspidiotus perniciosus.

Malus baccata var. *mandshurica* (Maxim.) Schneid.: Quadraspidiotus perniciosus.

Malus baccata sp.: Quadraspidiotus perniciosus.

Malus pumila Mill.: Eulecanium bituberculatum, E. coryli, Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus ostreaeformis, Q. perniciosus.

Malus pumila var. *Niedzwetzkyana* (Dieck.) Schneid.: Quadraspidiotus perniciosus.

Malus sylvestris (L.) Mill.: Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus ostreaeformis, Q. perniciosus.

Malus sp.: Epidiaspis leperii, Quadraspidiotus perniciosus.

Mespilus germanica L.: Quadraspidiotus perniciosus.

Morus alba L.: Eulecanium corni, Pseudaulacaspis pentagona.

Musci (*Mosses*): Newsteadia floccosa.

Odontites serotina (Lam.) Dum.: Orthezia urticae.

Parietaria officinalis L.: Orthezia urticae.

Parthenocissus tricuspidata (Sieb. et Zucc.) Planch.: Eulecanium corni, E. persicae.

Phragmites communis Trin.: Chaetococcus phragmitis.

Picea alba Mill.: Dynaspidiotus abietis.

Picea pungens f. *glauca* (Reg.) Beiss.: Dynaspidiotus abietis.

Picea sitchensis (Bong.) Carr.: Dynaspidiotus abietis.

Pinus mugo Turra: Leucaspis pusilla, Anamaspis loewi.

Pinus nigra Arn.: Leucaspis pini, L. pusilla, Anamaspis loewi, Lepidosaphes newsteadi.

Pinus ponderosa Dougl. ex Lawson: Leucaspis pini.

Pinus sylvestris L.: Leucaspis pini, L. pusilla, Anamaspis loewi.

Pinus tabuliformis Hort. ex Carr.: Leucaspis pini.

Platanus occidentalis L.: Eulecanium corni.

Platanus orientalis L.: Eulecanium corni.

Populus alba L.: Lepidosaphes ulmi, Chionaspis salicis, Quadraspidiotus gigas.

Populus berolinensis Dipp.: Quadraspidiotus gigas.

Populus canescens (Ait.) Smith: Pulvinaria betulae.

Populus nigra L.: Quadraspidiotus gigas.

Populus nigra var. *italica* (Münchh.) Koehne: Eulecanium corni, Pulvinaria betulae, Lepidosaphes ulmi, Quadraspidiotus gigas.

Populus trichocarpa Torrey et Gray ex Hook.: Quadraspidiotus gigas.

Populus sp.: Eulecanium corni, Lepidosaphes ulmi, Chionaspis salicis, Quadraspidiotus gigas.

Prunus amygdalo-persica (West.) Rehd.: Eulecanium corni.

Prunus amygdalus Batsch.: Eulecanium corni, E. prunastri, Quadraspidiotus perniciosus.

Prunus armeniaca L.: Eulecanium corni, E. prunastri, Lepidosaphes ulmi, Quadraspidiotus perniciosus.

Prunus avium L.: Eulecanium corni, Quadraspidiotus mařani, Q. ostreaeformis, Q. perniciosus.

Prunus baldschuanica Reg.: Eulecanium prunastri.

Prunus cerasifera Ehrh.: Eulecanium prunastri, Quadraspidiotus perniciosus.

Prunus cerasifera var. *atropurpurea* (Jaeg.) Rehd.: Eulecanium corni, E. prunastri, Quadraspidiotus ostreaeformis, Q. perniciosus.

Prunus cerasus L.: Quadraspidiotus ostreaeformis.

Prunus domestica L.: Eulecanium corni, E. coryli, E. prunastri, Pulvinaria betulae, Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus mařani, Q. ostreaeformis, Q. perniciosus, Q. pyri.

Prunus insititia L.: Epidiaspis leperii.

Prunus laurocerasus L.: Quadraspidiotus perniciosus.

Prunus mahaleb L.: Quadraspidiotus ostreaeformis, Q. perniciosus.

Prunus padus L.: Eulecanium corni, Quadraspidiotus perniciosus.

Prunus persica (L.) Batsch.: Eulecanium corni, E. prunastri, Quadraspidiotus perniciosus.

Prunus serotina Ehrh.: Quadraspidiotus perniciosus.

Prunus serrulata Lindl.: Quadraspidiotus perniciosus.

Prunus spinosa L.: Eulecanium corni, E. prunastri, Lepidosaphes ulmi, Epidiaspis leperii, Quadraspidiotus mařani, Q. ostreaeformis, Q. perniciosus.

Prunus sp.: Quadraspidiotus mařani, Q. ostreaeformis, Q. pyri.

Pyracantha coccinea Roem.: Eulecanium corni.

Pyrus elaeagrifolia Pall.: Epidiaspis leperii.

Pyrus nivalis Jacq.: Epidiaspis leperii.

Pyrus communis var. *pyraster* L.: Eulecanium corni, Pulvinaria betulae, Epidiaspis leperii, Quadraspidiotus ostreaeformis, Q. perniciosus.

Pyrus salicifolia Pall.: Epidiaspis leperii.

Pyrus communis var. *sativa* (DC.) DC.: Eulecanium corni, Pulvinaria betulae, Epidiaspis leperii, Quadraspidiotus mařani, Q. perniciosus.

Quercus alba L.: Eulecanium rufulum.

Quercus audleyensis Henry: Lepidosaphes ulmi.

Quercus castaneifolia C. A. Meyer: Eulecanium rufulum.

Quercus cerris L.: Acanthococcus roboris, Kermococcus roboris, Asterolecanium bellum, A. minus, A. variolosum, Eulecanium rufulum, Lepidosaphes ulmi, Chionaspis lepineyi, Diaspidiotus wünni, Targionia vitis.

Quercus lyrata Walt.: Asterolecanium bellum, A. minus.

Quercus palustris Münch.: Eulecanium rufulum.

Quercus petraea (Matt.) L. ex Liebl.: Acanthococcus roboris, Kermococcus quercus, K. roboris, Asterolecanium minus, A. querciola, A. variolosum, Eulecanium coryli, E. rufulum, Lepidosaphes ulmi, Chionaspis lepineyi, Quadraspidiotus lenticularis, Q. zonatus, Diaspidiotus hungaricus, D. wünni, Targionia vitis.

Quercus petraea f. *laciniata* (Lam.) Schwarz: Asterolecanium variolosum, Diaspidiotus wünni.

Quercus pubescens Willd.: Acanthococcus roboris, Kermococcus roboris, Asterolecanium bellum, A. minus, A. roboris, A. variolosum, Eulecanium rufulum, Lepidosaphes ulmi, Chionaspis lepineyi, Targionia vitis.

Quercus robur L.: Kermococcus roboris, Asterolecanium minus, A. variolosum, Eulecanium rufulum, Lepidosaphes ulmi, Chionaspis lepineyi, Quadraspidiotus zonatus, Diaspidiotus wünni, Targionia vitis.

Quercus robur f. *concordia* (Kirchn.) K. Koch: Asterolecanium variolosum, Eulecanium rufulum.

Quercus robur f. *fastigiata* (Lam.) Schwarz: Kermococcus quercus.

Quercus rubra L.: Asterolecanium variolosum, Eulecanium rufulum.

Quercus sp.: Eulecanium rufulum, Chionaspis lepineyi, Quadraspidiotus lenticularis, Diaspidiotus wünni.

Rhamnus cathartica L.: Quadraspidiotus ostreaeformis.

Ribes aureum Pursh.: Eulecanium corni, Lepidosaphes ulmi, Quadraspidiotus ostreaeformis, Q. perniciosus.

Ribes grossularia L.: Eulecanium corni, Quadraspidiotus ostreaeformis.

Ribes nigrum L.: Eulecanium corni, Quadraspidiotus ostreaeformis.

Ribes rubrum L.: Eulecanium corni, Pulvinaria betulae, Quadraspidiotus perniciosus.

Robinia pseudacacia L.: Eulecanium corni, Lepidosaphes ulmi.

Rosa canina L.: Eulecanium corni, Aulacaspis rosae, Quadraspidiotus perniciosus.

Rosa spinosissima L.: Eulecanium coryli.

Rosa sp.: Eulecanium corni, E. coryli, Lepidosaphes ulmi, Aulacaspis rosae, Quadraspidiotus perniciosus.

Rubus caesius L.: Aulacaspis rosae.

Rubus sp.: Eulecanium corni, Aulacaspis rosae.

Salix alba L.: Chionaspis salicis, Quadraspidiotus gigas.

Salix alba var. *vitellina* (L.) Stokes: Pulvinaria betulae.

Salix candida Flügge ex Willd.: Eulecanium corni.

Salix caprea L.: Chionaspis salicis.

Salix repens var. *rosmarinifolia* (L.) Wim. et Grab.: Pulvinaria betulae, Quadraspidiotus perniciosus.

Salix sp.: Eulecanium corni, Pulvinaria betulae, Lepidosaphes ulmi, Chionaspis salicis, Quadraspidiotus gigas, Q. perniciosus.

Sambucus nigra L.: Eulecanium corni.

Sanguisorba minor Scop.: Orthezia urticae.

Satureja vulgaris (L.) Fritsch.: Orthezia urticae.

Sophora japonica L.: Eulecanium corni.

Sorbus aucuparia L.: Epidiaspis leperii, Quadraspidiotus perniciosus.

Sorbus aucuparis var. *rossica* Späth. ex Koehne: Quadraspidiotus perniciosus.

Sorbus domestica L.: Epidiaspis leperii, Quadraspidiotus perniciosus.

Sorbus torminalis (L.) Crantz: Pulvinaria betulae, Quadraspidiotus ostreaeformis.

Spiraea salicifolia L.: Lepidosaphes ulmi.

Symphoricarpos albus (L.) Blake: Eulecanium corni.

Symphoricarpos albus var. *laevigatus* (Fern.) Blake: Eulecanium corni, Lepidosaphes ulmi.

Syringa vulgaris L.: Lepidosaphes conchyformis, L. ulmi, Quadraspidiotus ostreaeformis, Q. perniciosus.

Tamarix gallica L.: Eulecanium corni, Lepidosaphes ulmi.

Tamarix tetranda Pall.: Lepidosaphes ulmi.

Tamarix sp.: Eulecanium corni.

Taxus baccata L.: Eulecanium crudum.

Teucrium chamaedrys L.: Orthezia urticae.

Thuja occidentalis L.: Eulecanium arion, Carulaspis visci.

Tilia cordata Mill.: Eulecanium corni, E. coryli, Quadraspidiotus ostreaeformis.

Tilia platyphyllos Scop.: Eulecanium corni, Quadraspidiotus ostreaeformis, Q. perniciosus.

Tilia platyphyllos f. *laciniata* (Loud.) V. Engler: Lepidosaphes sp., Quadraspidiotus ostreaeformis.

Tilia tomentosa Moench: Lepidosaphes sp.

Tilia sp.: Eulecanium corni, E. coryli, Lepidosaphes ulmi, Lepidosaphes sp., Quadraspidiotus ostreaeformis.

Ulmus americana L.: Gossyparia spuria.

Ulmus carpinifolia var. *Dampieri* (Wesm.) Rehd.: Lepidosaphes conchyformis.

Ulmus carpinifolia f. *Wredei* (Jühlke) Rehd.: Lepidosaphes conchyformis.

Ulmus glabra Huds.: Gossyparia spuria, Lepidosaphes conchyformis.

Ulmus glabra f. *atropurpurea* (Späth) Rehd.: Eulecanium corni.

Ulmus glabra f. *exoniensis* (K. Koch) Rehd.: Gossyparia spuria, Eulecanium corni.

Ulmus glabra f. *pendula* (Loud.) Rehd.: Gossyparia spuria, Eulecanium corni.

Ulmus procera f. *Vanhouttei* (Schelle) Rehd.: Quadraspidiotus perniciosus.

Ulmus sp.: Gossyparia spuria, Eulecanium corni, Lepidosaphes conchyformis, L. ulmi, Quadraspidiotus perniciosus.

Urtica dioica L.: Orthezia urticae.

Vaccinium myrtillus L.: Lepidosaphes ulmi.

Viburnum opulus L.: Quadraspidiotus ostreaeformis.

Vitis vinifera L.: Eulecanium corni, Pulvinaria betulae, Quadraspidiotus perniciosus.

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GYNANDROMORPHS OF BYRSOTRIA FUMIGATA (GUÉRIN) (BLATTARIA: BLABERINAE)[1]

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ABSTRACT

An individual, remarkable in displaying gynandromorphism in its external morphology as well as in its primary sex organs, is described in detail. On its left side the head was larger; the legs stouter; the base of the pronotum angular; the tegmen brachypterous and the wing greatly reduced; the abdomen, cerci, and external and internal genitalia characteristically female. On its right side the head and legs were smaller; the base of the pronotum rounded; the tegmen macropterous and the wing relatively large; the abdomen, cerci, and external and internal genitalia characteristically male. Comparisons with normal insects are made and illustrated. An addendum describes a second gynandromorph, discovered after the account of the first one was in press.

Gynandromorphism has been observed, not infrequently, in the following families of orthopteroids: Tettigoniidae, Phasmidae, Gryllidae frequently, in the following families of orthopteroids: Tettigoniidae, Phasmidae, Gryllidae (Chopard 1938), and Acrididae (Severin 1943). However, so far as we know, the only previous records of gynandromorphs in the Blattidae are a specimen of *Periplaneta americana* (L.), which had ovum-like bodies in its testes (Thirumalacher 1928), and males of *Blattella germanica* (L.), in which the anlagen of the gonads were claimed to be normally "hermaphroditic" (Heymons 1890). Heymons stated that the testes of *B. germanica* are formed from only part of the genital anlagen and that the remainder develops, to varying degrees, into rudimentary female sex glands. He described several specimens, one being a mature male which had two partly developed ovaries. In *B. germanica* and *P. americana* gynandromorphism was only evident in the internal sex organs, whereas in the specimen of *Byrsotria fumigata*[3] described below, the anomaly was expressed externally by secondary sexual characters as well as internally by the sex organs.

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[3]We are indebted to Mr. James A. G. Rehn, The Academy of Natural Sciences of Philadelphia, for identifying this species, for reading the manuscript, and for calling our attention to the Severin (1943) reference. The taxonomy of this Cuban cockroach has been treated by Rehn and Hebard (1927).

OBSERVATIONS

A gynandromorph of *Byrsotria fumigata* was discovered in our laboratory colony when it completed its imaginal molt on June 19, 1958. This insect was observed daily thereafter, until on July 25 it was seen to behave like an ovipositing female; that is, it periodically pushed apart its terminal sternal and tergal plates so that the genital cavity was alternately exposed, then closed again. This behavior continued throughout the remainder of the day, but the insect did not form an oötheca. The following day the gynandromorph was dissected; no oötheca was found in its brood sac, but about a dozen mature eggs from its left ovary were found free in the body cavity.

Sexual dimorphism is pronounced in *Byrsotria fumigata* (plate I, A, C), so, because of this, the gynandromorph (plate I, B) presents a particularly striking appearance. The gynandromorph is differentiated bilaterally according to sexual characters; its left side is like that of the female, but its right side is predominantly like that of the male. The overall size of the insect is very similar to that of the female. Because the tegmina of the macropterous male extend

well beyond the end of its abdomen, the male body is even smaller in comparison with the female than it appears in plate I. Relative sizes of the abdomens of male, female, and gynandromorph are shown in plate IV.

HEAD.—The head of the gynandromorph plate II, B) is asymmetrical, the right side being smaller and more nearly male-like than the left side. Obvious sexual dimorphism exists in the following features of the gynandromorph, which may be compared with those of the male and female (plate II, A, C): (1) The right ocellus lies close to the antennal scrobe, as in the male; the left ocellus is further from the antenna, as in the female. (2) The right mandible is smaller than the left. (3) The right side of the labrum is smaller than the left. The sculpturing of the face is more rugose than in either the male or the female.

THORAX.—*Legs*.—The most pronounced differences are in the coxae, femurs, and the spines on the tibiae; these structures on the female-like left side of the gynandromorph are stouter and longer than those on the right. However, the legs on the right side are somewhat longer and stouter than those of the smaller male.

Pronotum (plate III).—The overall size and shape of the pronotum of the gyandromorph are similar to that of the female:

Sex	Size in Millimeters		No. of Insects
	Width	Length	
Gynandromorph...	20.5	12.5	1
Female.....	21.2±0.39[a]	13.6±0.21	10
Male.....	14.2±0.15	10.0±0.10	10

[a]Standard error of the mean.

The anterior margin is broadly rounded on the left side, as in the female, but more narrowly curved on the right. The angle of the base with the lateral margin approaches a right angle on the left side, as in the female, whereas on the right the lateral margin curves sharply into the base, similar to the pronotum of the male. The translucent buff band along the anterolateral margin is broad on the left, as in the female, but narrower on the right.

Tegmina (plate I).—The right tegmen is over twice as long as broad, similar to that of the macropterous male. The following differences from the male tegmen were noted: The posterior margin of the right tegmen is broadly emarginated distal to the anal field; it is torn and crumpled from this notch to the apical margin. The apex is also crumpled. The left tegmen is brachypterous and typically female.

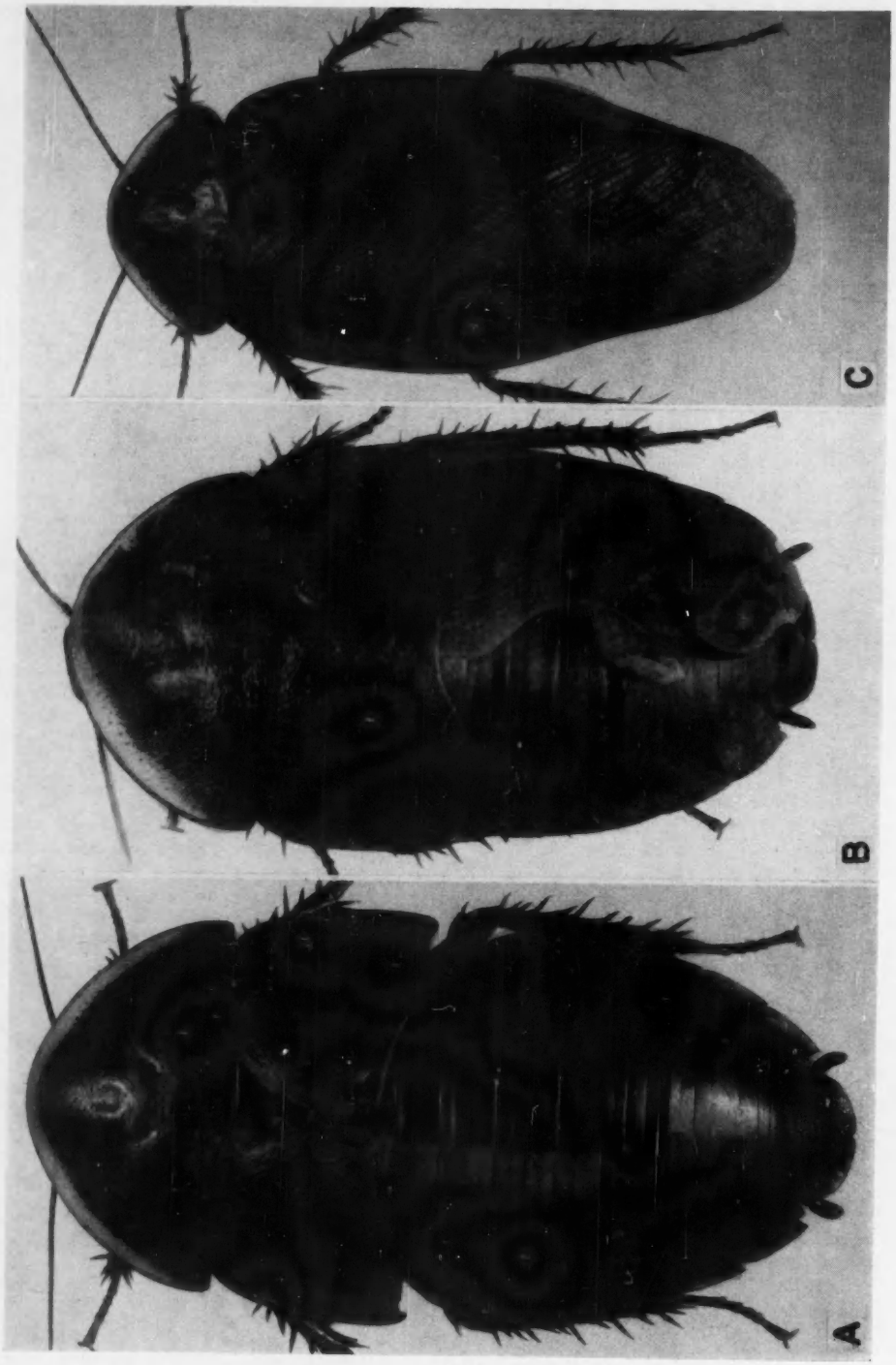
Wings.—The right wing is typically male; the preaxillary area is moderately developed; the apical end is crumpled and the apical margin is missing, apparently broken off; the anal area is much reduced. The left wing is greatly reduced and typically female.

ABDOMEN.—*Dorsum*.—An excised portion of the dorsum, minus the lateral ends of the abdominal terga, is shown in plate IV, B. The left sides of these terga may be seen in plate I, B. Comparable terga of the female and male (wings removed) are shown in plate IV, A, C. A sharp line of demarcation divides the dorsum of the gynandromorph abdomen into distinct male (light brown) and female (dark brown) sides. Laterally, the cuticle of the right side of each tergum is sculptured in low relief similar to, but not identical with, that of the male. The cuticle of the left sides of the terga is female-like but considerably more rugose. The apical lateral corners of terga one through four on the right side are male-like, but the corners of terga five through seven on the right and two through seven on the left are elongated posteriorly, as in the female. The supra-anal plate (tenth tergum) is essentially female-like. The supra-anal plates of the male and female are compared in plate VI, F, G.

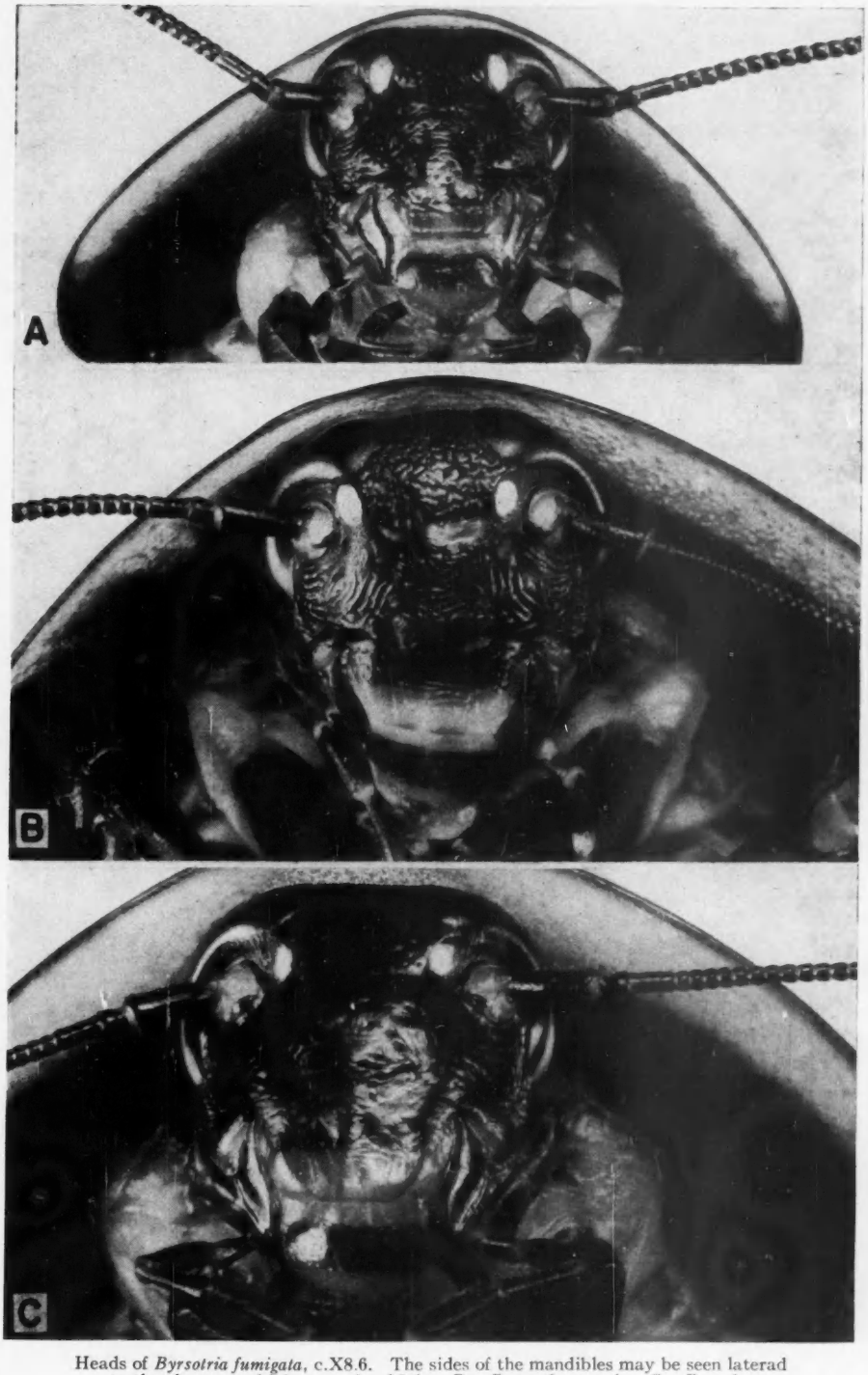
Cerci.—The male cerci are longer, more conical, and more obviously segmented than those of the female (plate IV; plate VI, F. G). The right cercus of the gynandromorph (seen from below in plate IV, D) is typically male, whereas the left cercus is short, broad, and typically female.

Venter (plate IV, D, E, F, G).—The sculpturing of the cuticle on the right side of the venter, up to and including the sixth segment, is male-like. The left side is typically female except that the apical halves of the sterna are more rugose. The seventh sternum of the female and the ninth sternum of the male are the subgenital plates; that of the female is large and symmetrical, whereas that of the male is small, asymmetrical, and bears a short stylus just medial to the left cercus and a long stylus close to the right cercus (plate IV, E; plate V, C). The seventh sternum of the gynandromorph (plate IV, D) is a highly modified subgenital plate: it is narrow (male-like) on the right, but wider (female-like) on the left. The cuticle is much more rugose than in either male or female. Rudiments of the eighth and ninth male-like sterna, which were partly concealed beneath the seventh sternum, are described with the external genitalia.

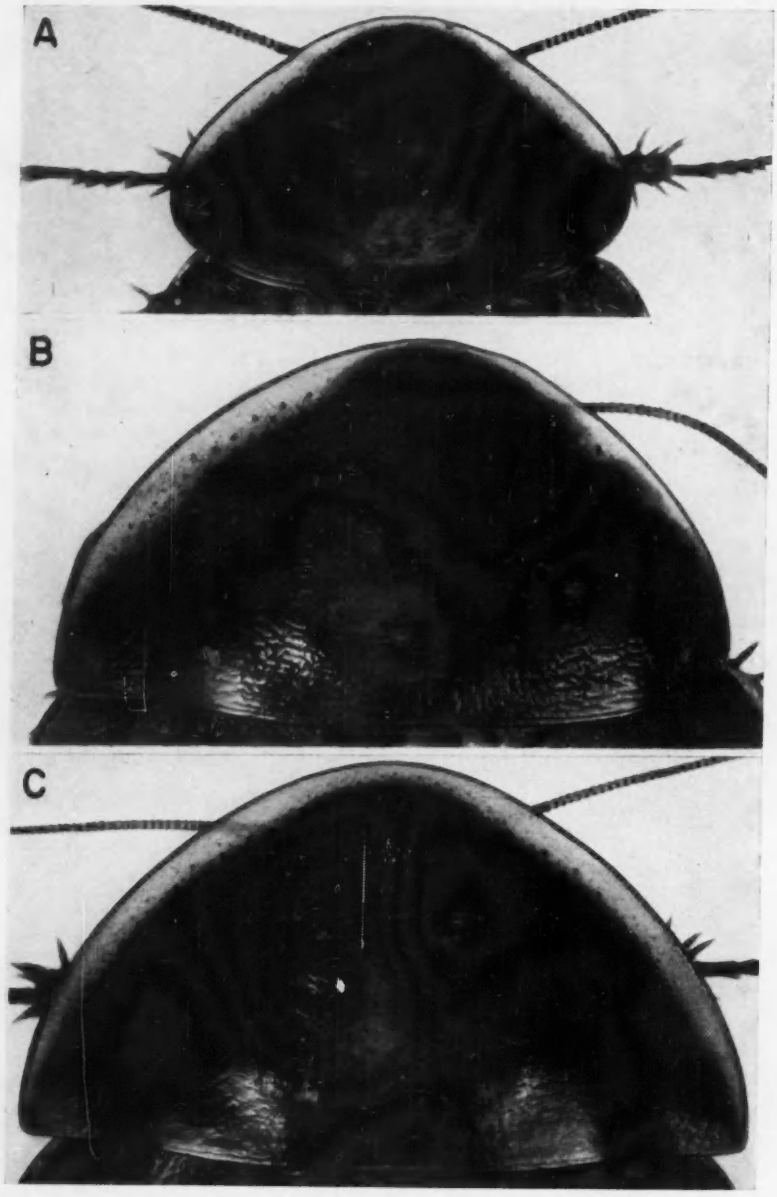
EXTERNAL GENITALIA.—***Female*** (plate V, A).—Medially within the genital cavity, between the tenth tergum and seventh sternum, lies the ovipositor; it is composed of three sets of paired valvulae of which only the first and third pair can be seen; the second valvulae lie concealed behind the first pair. Dorsal to and behind the ovipositor, just beneath the supra-anal plate, are a pair of symmetrical paraprocts. Below and anterior to the ovipositor is the rugose brood sac, which is shown everted in the figure.



Byrsotria fumigata, c.X2.7. A.—Female. B.—Gynandromorph. C.—Male.



Heads of *Byrsotria fumigata*, c.X8.6. The sides of the mandibles may be seen laterad to the clypeus and labrum. A.—Male. B.—Gynandromorph. C.—Female.



Pronotums of *Byrsotria fumigata*, c.X5.1. A.—Male. B.—Gynandromorph. C.—Female.

Male (plate V, C).—The phallic structures of this species occur as three distinct lobes. Located medioventrally in the genital cavity, between the tenth tergum and ninth sternum, is the membranous penis. A semicircle of short, stout spines surrounds the ventral edge of the penis; mesad to this row of spines, the penis is invaginated. A flat, narrow sclerotized rod lies along the dorsal surface of the penis; the distal end of this rod expands into an irregularly shaped, free-standing plate which lies in the invagination of the penis (plate VI, F). To the right of the penis is an extensible, hooked right phallomere; although shown partly extruded in the figures (plate V, C; plate VI, F), this phallomere is normally retracted within a membranous tube formed by its proximal attachment. To the left of the penis is a complex, three-lobed left phallomere, which is intricately sclerotized. Dorsal to and behind the phallic lobes are two asymmetrical paraprocts. Proximally, the medial end of the sclerotized part of the right paraproct is modified into a strong hook. The corresponding part of the left paraproct is membranous, but projecting medially from the sclerotized base is a small, straight, finger-like process.

Gynandromorph (plate V, B).—The right side has both male and female characters. The left side is entirely female-like; on the left are a typical female left paraproct, the three left valvulae of the ovipositor, and a small brood sac. On the right side are three sclerotized processes that are obviously rudiments of the right valvulae. Recognizably male-like characters on the right side are the right paraproct, with sclerotized hook (see also plate IV, D); the right half of a narrow eighth sternum; and the incompletely sclerotized right half of a ninth sternum, which bears the right stylus. An unidentifiable sclerotized lobe lies to the right of the midline, below and anterior to the rudiments of the right side of the ovipositor; probably this structure is a rudiment of one of the phallic lobes.

INTERNAL GENITALIA.—*Female* (plate VI, A).—Paired ovaries are connected by oviducts to the median oviduct above the anterior end of the brood sac. On each side of the median oviduct is a lobe of the left colleterial gland, which is composed of many large, branched tubes. Between the lobes of the left gland is the right colleterial gland, a compact mass of coiled, branched tubules (plate VI, B). Beneath the colleterial glands on each side of the median oviduct is a spermatheca and its accessory gland.

Male (plate VI, D).—The only structures described from the male are those organs homologous with identifiable organs in the gynandromorph. The prominent accessory glands open into the anterior end of the ductus ejaculatorius. These glands are predominantly long, unbranched tubes which conceal a smaller mass of much shorter tubes. The accessory glands secrete material that forms the spermatophore. The ductus ejaculatorius of the illustrated specimen (see arrow) is partially distended, presumably with accessory gland secretion.

EXPLANATION OF PLATES IV, V, and VI.

PLATE IV

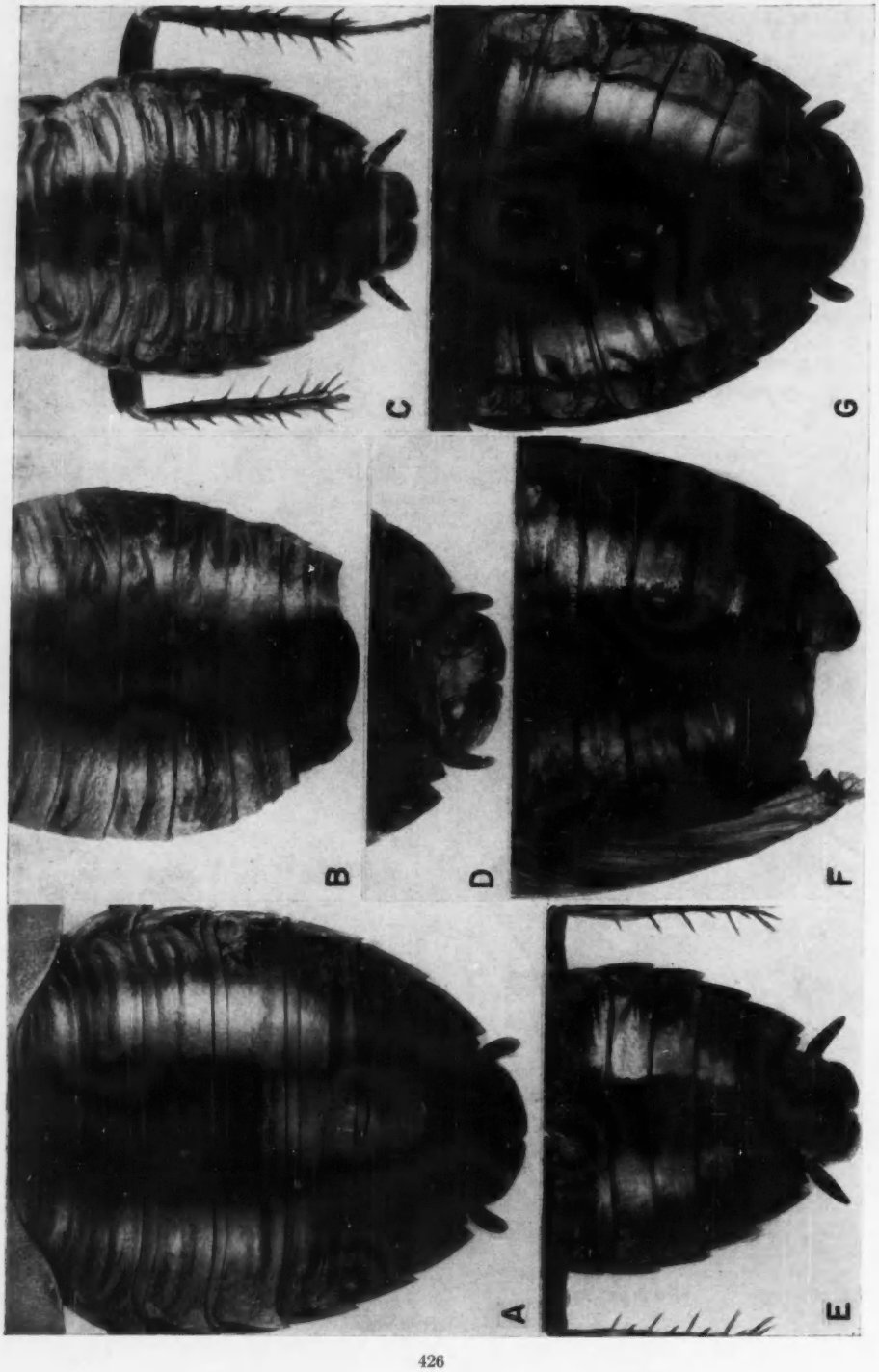
Abdomens of *Byrsotria fumigata*, c.X3.2. A.—Female dorsum. B.—Gynandromorph, excised terga three through nine. C.—Male dorsum. D.—Gynandromorph, seventh sternum and supra-anal plate from below. Note the hooked, male-like right paraproct (compare with Plate V, C); the conical, male-like right cercus; and the blunt, female-like left cercus. E.—Male venter. F.—Gynandromorph venter after dorsum had been removed. G.—Female venter.

PLATE V

External genitalia of *Byrsotria fumigata*, c.X9.3. A.—Female genital cavity from below. The light colored brood sac has been everted. B.—Gynandromorph genital cavity from below. On the upper left is the female-like left paraproct. Beneath this is the ovipositor. At the lower left, below the base of the left side of the ovipositor, is the brood sac. On the upper right is the male-like, hooked, right paraproct. Below this is part of the male-like ninth sternum, bearing a stylus. The narrow, male-like eighth sternum is the black band beneath the right side of the ovipositor and the ninth sternum. C.—Male genital cavity from the rear; the super-anal plate has been elevated and the subgenital plate depressed.

PLATE VI

A to E, internal genitalia of *Byrsotria fumigata*. A.—Virgin female about the same age as the gynandromorph, dorsal view, c.X3. The ovaries are the large lateral organs. The lobes of the left colleterial gland are immediately behind the oviducts. The right colleterial gland is between the lobes of the left gland (see also figure B). B.—Central part of preparation in figure A stained with hematoxylin, c.X6. The arrow at lower right indicates right colleterial gland. The arrow at upper left indicates a spermatheca. The tube with the bulbous end just to the right of the spermatheca is a spermathecal gland. C.—Gynandromorph, dorsal view, c.X4. The longitudinal axis approximately parallels the arrow. The detached, right ovary is misplaced to the left of the left ovary. Empty follicles, which had contained the eggs found free in the body cavity, are visible along the left side of the left ovary. The arrow indicates the ductus ejaculatorius with attached, male-like accessory glands. At the left of the male-like organs is the left colleterial gland. D.—Male, dorsal view, c.X6. The arrow indicates the ductus ejaculatorius. Posteriorly the left phallomere, the penis, and the retracted right phallomere can be seen. E.—Gynandromorph, c.X6. Part of the preparation in figure C with male-like organs removed. The arrows indicate the spermatheca-like structures. The base of the lower left arrow arises in the lumen of the severed hind gut. The lobe on the upper right is the brood sac. F.—Male terga, seven through ten, c.X3.2. The penis and the partly extruded, hooked right phallomere extend behind the tenth tergum. G.—Female terga, seven through ten, c.X3.2.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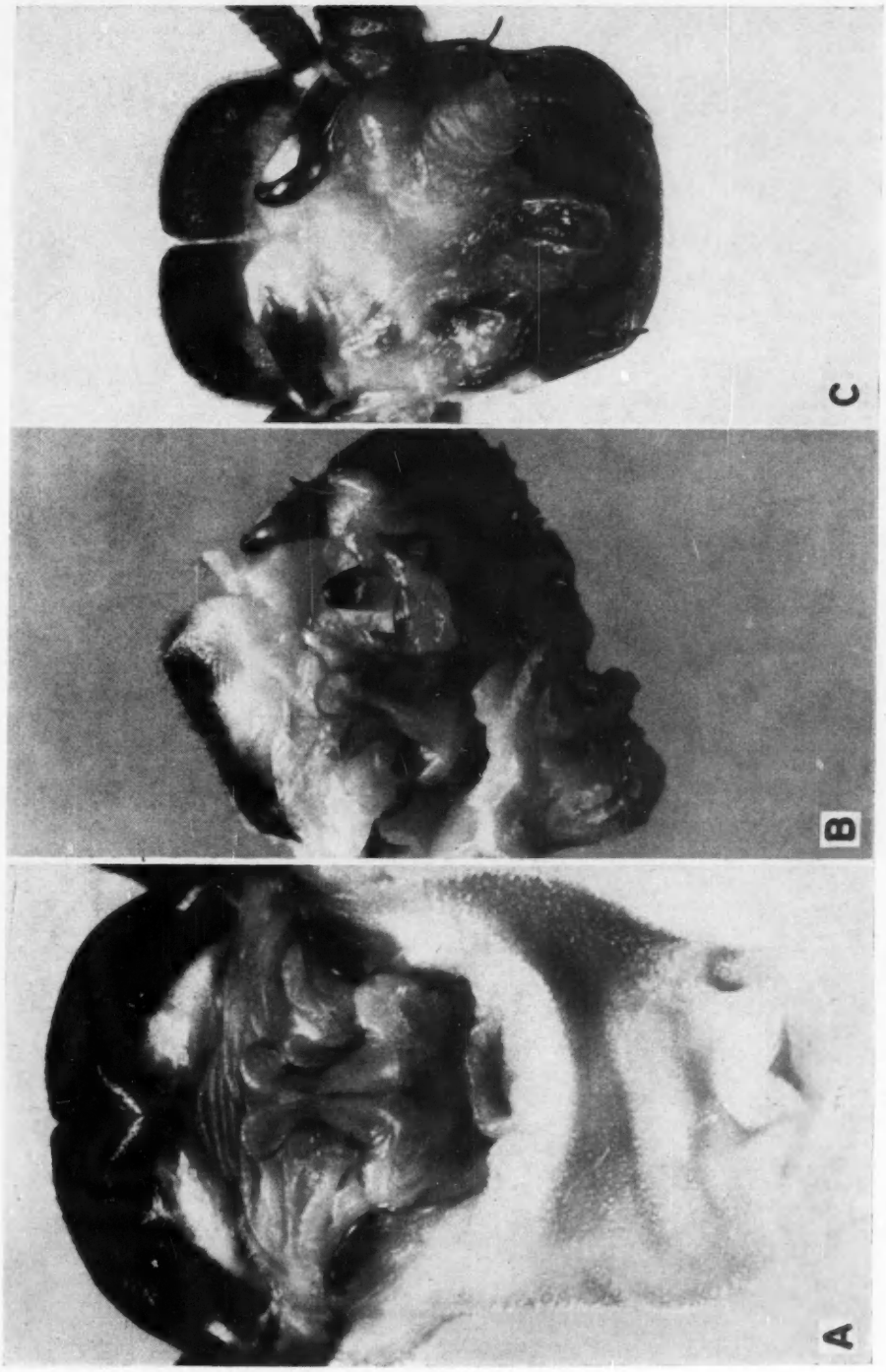
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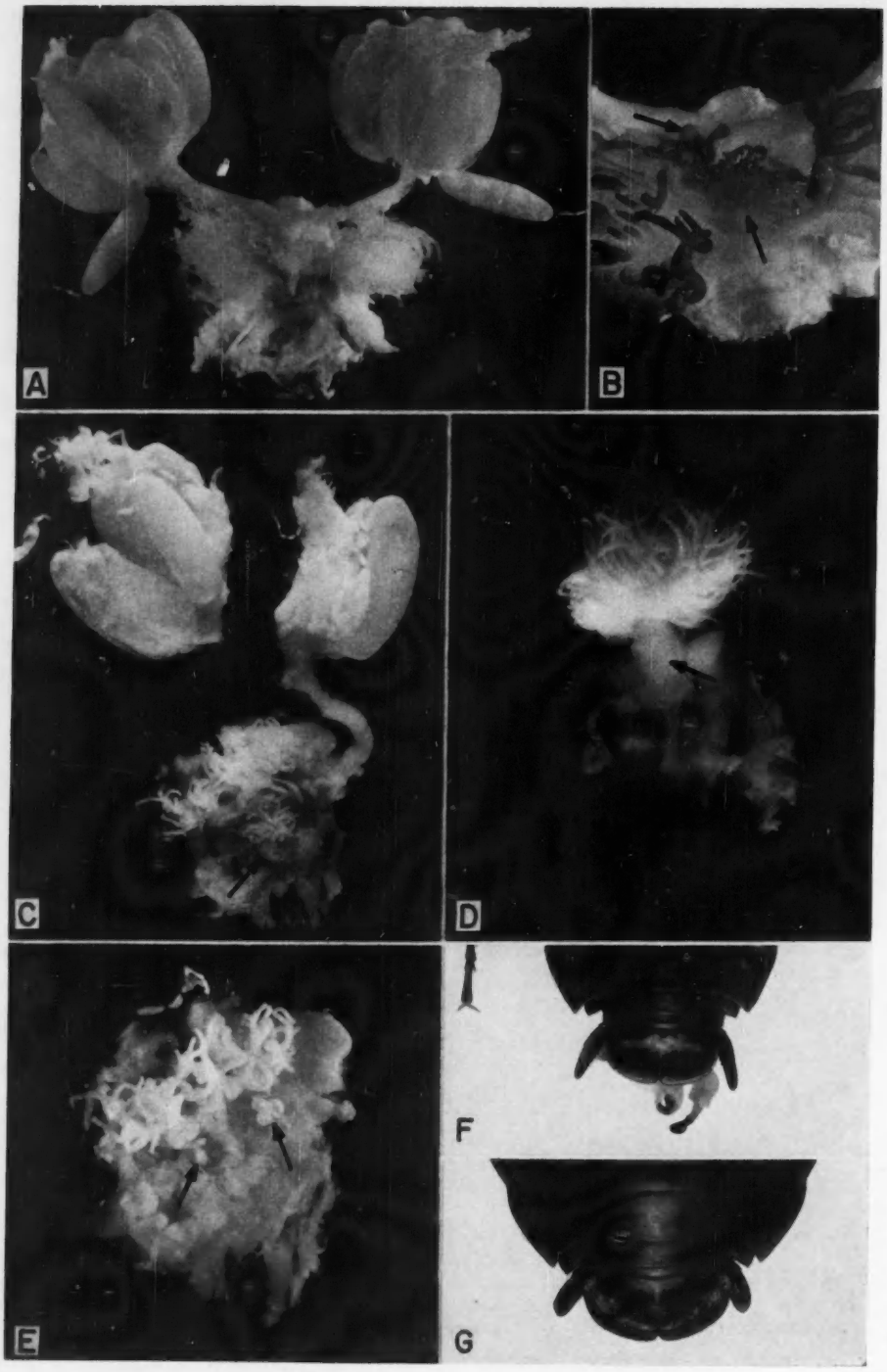
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Gynandromorph (plate VI, C, E).—The reproductive tract is predominantly female. A small brood sac is present (see also plate V, B). There are two ovaries, both of which contain mature eggs as well as smaller oöcytes. Only the left ovary joins an oviduct posteriorly. The right ovary (misplaced to the left of the left ovary in figure C) was connected to the posterior part of the tract by only a thin strand of tissue; this connection may have been a rudiment of the right oviduct or, perhaps, a male vas deferens. Only a portion of the left colleterial gland is present. The right colleterial gland is apparently missing, as are the testes. A cluster of short, unbranched tubes apparently represents the male accessory glands; these are attached to a ductus ejaculatorius (arrow, plate VI, C); this duct is distended, as though with accessory gland secretion. Beneath the male-like organs are small, lobed structures that undoubtedly represent the spermathecae and spermathecal glands (arrows, plate VI, E).

ADDENDUM

After the above account was in press a second gynandromorph of *Byrsotria fumigata* was found in our laboratory colony. Externally the dimorphism between the male and female sides of the second specimen is much less obvious than in the first. In the second specimen the male-like structures are on the left side rather than on the right as in the first. The following is a description of this second gynandromorph.

Head.—Very slightly asymmetrical, the left side being smaller than the right.

Thorax.—Legs: Similar on both sides of the body except that the left pro- and mesothoracic coxae are slightly smaller than those on the right. *Pronotum:* Female-like, but the left side is slightly smaller than the right. The buff-colored, lateral margin is slightly narrower on the left than on the right. *Tegmina:* Both are abnormal and incompletely expanded. The apical edge of the left tegmen is produced posteriorly into a sinuously edged lobe, making it longer than the normal female tegmen. *Wings:* Both are reduced in size and female-like.

Abdomen.—No differentiation of terga or sterna, except the subgenital plate, from normal female. *Cerci:* Left cercus typically male, right female. *Seventh sternum:* The subgenital plate is typically female on the right but modified from the female shape on the left by a shallow notch in the apical edge from the midline toward the left; the notch is about one fourth the width of the sternum and half as deep as wide. This notch exposes the male-like genital lobes which first drew our attention to this anomalous individual.

External Genitalia.—In the genital cavity sclerotized lobes on the left side are identifiable as male structures. One lobe bears a stylus and is obviously a rudiment of the male ninth sternum. To the right of this is a knob that may be referable to the hooked right phallomere. The penis is present as is the ovipositor. The ovipositor valvulae on the right side are normal; however, the second and third valvulae on the left are abnormal, their distal ends being twisted and bent. The right paraproct is typically female, but that on the left bears a sclerotized, hooked process; this latter is male-like but not typically so.

Internal Genitalia.—Male accessory glands and ductus ejaculatorius are present in the left side of the abdominal cavity. The testis, if present, was lost in dissection. The right ovary and oviduct are present together with a spermatheca and its accessory gland. Right and left colleterial glands are also present.

Both gynandromorphs have been deposited in the United States National Museum.

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NOTICE TO MEMBERS

Authors are urged to consult the latest revised list of "Common Names of Insecticides." See Journal of Economic Entomology 52(2): 361–362. April 1959.

The Chemical definition of each insecticide, the name of which does not appear in this list, should be given the first time the name occurs in a manuscript accepted for publication by the Entomological Society of America; also in the abstract.

THE LARVAE OF POMPILIDAE (HYMENOPTERA)[1]

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ABSTRACT

The larvae of only about ten species of Pompilidae have been described, and no attempts have ever been made to make a comparative study to see what characters of classificatory value the larvae may offer. In this paper the larvae of 21 North American species belonging to 9 genera and subgenera are described for the first time, and the published descriptions (which include members of three additional genera) are reviewed. This is still too poor a representation to permit many conclusions regarding the evolution or the major phyletic lines of the Pompilidae. It does, however, permit one to make certain generalizations regarding family characters which will serve to separate the larvae of Pompilidae from those of other digger wasps. Chief among these is the fact that the second pair of thoracic spiracles is vestigial. Within the family, one finds only nebulous differences between the two major subfamilies, the Pepsinae and the Pompilinae. However, certain complexes of genera do stand together as they do on adult structure. A general trend in the reduction of the mandibular dentition can be noted in the Pompilinae. It seems probable that larval characters may someday prove of considerable value in helping to classify these wasps, and the collection and description of the larvae of additional species is urgently needed.

Although the family Pompilidae includes nearly 2,000 species, the larvae of only about 10 of these have ever been adequately described; this 10 includes none of the approximately 250 Nearctic species. The few described larvae have never been compared with one another to see what the comparison might yield in the way of additional taxonomic characters for this difficult group of wasps. Nor has anyone, so far as I know, presented characters which will separate the larvae of Pompilidae from those of other wasps.

The present study is no more than an introduction to the subject. It includes descriptions of the larvae of 21 North American species belonging to 9 genera and subgenera, plus a brief review of the the published descriptions (which include members of 3 additional genera). Despite this still very poor representation, it is possible to point out certain characters which will, as far as now known, always separate the larvae of Pompilidae from those of other wasps. It is also possible to draw a few preliminary conclusions about the use of larval characters in the taxonomy of these wasps.

Many of the larvae described here were collected by C. M. Yoshimoto and myself in the course of biological studies. Additional specimens have been supplied by F. X. Williams and K. V. Krombein, both of whom have published extensively on the biology of Pompilidae. The drawings of whole specimens were done by Enrico Sismondo; all the remaining drawings were made by myself, with the aid of a microprojector, from material cleared in potash and mounted in glycerin. All descriptions pertain to fully grown, nondiapausing specimens, except where otherwise stated.

STRUCTURE OF POMPILID LARVAE

The following description is drawn from all larvae seen and from all published descriptions. It is probable that when the larvae of more genera and species are known, exceptions will be found to some of these statements.

Body.—More or less fusiform, somewhat flattened ventrally, with a series of rounded pleural lobes on all segments except the last; each segment except the last divided into two annulets dorsally by a more or less distinct transverse crease; anus transverse, terminal or nearly so, directed caudad. Integument whitish, with minute transverse wrinkles, some genera with minute spinules on parts of the venter, many genera with inconspicuous small setae on parts of the dorsum. Second pair of thoracic spiracles vestigial, much smaller than the other nine pairs and sometimes difficult to see at all (see fig. 12b as compared with 12a); other spiracles of complex structure, differing greatly in different genera; peritreme very narrow; walls of atrium weakly to strongly spinose; opening into subatrium and walls of subatrium with various types of spines and prominences.

Head.—Wider than high; parietal bands present, often long and heavily pigmented; epistomal suture not distinct; coronal suture weak or absent. Antennal orbits circular or nearly so; antennal papillae present, large or small, bearing three small sensory cones at their tip. Head setae present, varying considerably in length and in distribution. Head lightly if at all pigmented, but often with weak brownish spots on the front and clypeus in addition to the usually dark parietal bands.

Mouthparts.—Labrum with two large lateral lobes and a smaller median lobe, its margin weakly if at all bristly, but with a series of fairly prominent sensory cones; disc of labrum generally with an irregular transverse row of setae and some additional, nonsetigerous punctures. Epipharynx with dense, small spinules on the median lobe, elsewhere with rather evenly distributed larger

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spinules and/or papillae. Mandibles strong, more or less pigmented, not more than twice as long as their maximum width, the base usually with one or more lateral setae; apex typically with three teeth which tend to surround a ventral concavity, the apical two teeth sharp, the basal tooth broad and blunt (in one genus, *Anoplius*, the basal two teeth are confluent, as in fig. 47; in the genus *Homonotus* the mandibles are edentate, fig. 51). Hypopharynx spinulose, bilobed. Maxillae setose laterally, more or less spinulose and often somewhat produced on the inner apical margin (the "lacinial area"); palpi and galeae of approximately equal length, the latter more slender and terminating in fewer (one to three) sensory cones. Labium of moderate breadth, with some ventral and apical setae; palpi short; surface of labium somewhat produced around the spinneret, the latter a transverse opening of moderate width which is more prominent on the sides than medially.

SUBFAMILY PEPSINAE

The larvae of this subfamily are strikingly similar to those of the Pompilinae, and I am unable to present any clear-cut characters for separating them. In all pepsine larvae that I have seen, body setae are absent or restricted to a few minute ones on the prothoracic dorsum. Many pepsine larvae possess minute spinules on the venter. Head setae are generally short, the longest setae no more than one-third as long as the diameter of the antennal orbit (see table I). The genus *Auplopus* may be an exception; at least Grandi (1926) figures the head setae of *A. carbonarius* as being nearly as long as the diameter of the orbit. The mandibles of Pepsinae show relatively little variation; in all of them there are three apical teeth, the innermost one broad and generally truncate.

Genus **Pepsis** Fabricius

In this genus the spiracles are elliptical and of very complex structure, with the opening into the subatrium slitlike; the antennal papillae are unusually small; the parietal bands are short; the mandibles are nearly or fully twice as long as wide and the three teeth are in nearly the same plane; the spinneret has a group of three or four setae close beside it on each side.

Pepsis thisbe Lucas

(Figs. 1 to 7, 40)

Williams (1956) has discussed the biology of this species, including a brief description of the larva, several figures, and one photograph. The more detailed description below is drawn from two of Williams' specimens, one a last-instar larva preserved in alcohol, the other a complete larval integument taken from a cocoon. These specimens are from La Mesa, San Diego Co., California, and were taken in 1954.

Body.—Length 25 mm.; maximum width 10.5 mm. (fig. 7). Somewhat depressed, the venter quite flat; pleural lobes strong on all segments, but especially so posteriorly; apical abdominal segment somewhat truncate, the anus somewhat below the middle of the segment. Spiracles vertically elliptical, the second thoracic spiracles very much smaller than the others; anterior thoracic spiracles 0.17 mm. in maximum diameter, the atrium lined with long sharp spines which give way inwardly to branching spines; opening into subatrium an elongate slit guarded by many spinose processes; subatrium swollen, its walls lined with spines in series (figs. 5, 6). Integument without noticeable spines or setae.

Head.—Width 2.5 mm.; height 2.3 mm. (fig. 1).[2] Parietal bands 0.6 mm. long, linear, brown; antennal orbits 140μ in diameter; antennal papillae very small, about 25μ in length (fig. 2); head setae sparse and small, the longest ones only 30μ long. Labrum 1.1 mm. wide, 0.35 mm. in median height; surface with about 12 weak setae and 18 submarginal sensory cones with pigmented rims; median apical lobe small, its surface and margin bristly; epipharynx entirely covered with small spinules which are denser and sharper medio-apically than elsewhere (fig. 4). Mandibles 1.2 mm. long, 0.6 mm. in maximum width; apex with three teeth which are in about the same plane, the inner tooth broad and blade-like; ventral surface excavated beneath the teeth; dorsal surface somewhat gibbous about two-thirds the distance from the base, but without any noticeable setae (fig. 40). Maxillae with numerous lateral setae, the lacinial area somewhat produced, clothed with small spinules; palpi 130μ long, terminating in six small sensory cones, one of which is much larger than the others; galeae 145μ long, terminating in three small sensory cones. Prementum of labium rather broad; palpi about 100μ long; spinneret with a group of four setae on each side (fig. 3).

Pepsis mexicana Lucas

(Fig. 41)

My description of this species is drawn from a single badly molded specimen taken from a cocoon sent to me by F. X. Williams from La Mesa, Calif. Williams (1956) has discussed the biology and immature stages.

Body.—Length about 20 mm. Form apparently not dissimilar to that of *thisbe*. Spiracles elliptical, the second thoracic spiracles minute.

Head.—Setae small, the longest ones measuring 50μ. Antennal orbits 140μ in diameter; antennal papillae slightly longer than thick, measuring about 35μ. Labrum 0.95 mm. wide; median lobe small, bristly; surface with an irregular series of

[2]Head height, here as elsewhere in this paper, is measured on the median line, exclusive of the labrum and other mouthparts. Head width is measured at its maximum point.

Table 1.—Ratios and setal counts for some species of Pompilidae (mature larvae)

Species	Ratios[a]			Setal counts[b]			
	HW/HH	ML/MW	LS/OD	Cly.	Lab.	Man.	Spin.
PEPSINAE							
Pepsis thisbe Lucas	1.09	2.0	.22	14	12	0	4
P. mexicana Lucas	——	1.9	.25	16	20	3	3
Hemipepsis ustulata ochroptera Stål	1.15	1.65	.24	8?	0?	2	14
Priocnemis minorata Banks	1.23	1.68	.30	28	12	2	1–2
P. cornica Say	1.12	1.58	.33	10	10	1	1
Dipogon sayi sayi Banks	1.22	1.55	.33	8	10–12	2	0
D. papago anomalus Dreisbach	1.17	1.58	.33	8	10	1	0
Auplopus carbonarius (Scopoli)	1.20	1.40	——	8	18	1	0?
POMPILINAE							
Poecilopompilus i. interruptus (Say)	1.13	1.78	.67	10	16–18	2–3	9
Batozonellus lacerticida (Pallas)	1.30	1.52	——	18	24	4	12
Episyron q. quinquenotatus (Say)	1.22	1.57	.78	12	14	1	7
E. posterus (Fox)	1.25	1.58	.80	12	12	1	7
Anoplius (Anoplius) illinoensis (Rbt.)	1.30	1.62	.50	14	10	2	2
A. (A.) virginiensis (Cresson)	1.35	1.55	.50	14	10	2	2
A. (A.) ithaca (Banks)	1.25	1.55	.57	—	10	2	3
A. (Pompilinus) fraternus (Banks)	1.25	1.40	.75	14	12	4	3
A. (P.) marginatus (Say)	1.22	1.45	.40	10	12	2	3
A. (P.) subcylindricus (Banks)	1.22	1.53	.50	12	12	3	3
A. (P.) krombeini Evans	1.20	1.48	.50	10	10	2	3
A. (Arachnophroctonus) marginalis (Bks.)	1.23	1.60	.80	28	18	4–5	5
A. (A.) semirufus (Cresson)	1.32	1.60	.56	14	10	2	3
A. (A.) apiculatus autumnalis (Bks.)	1.30	1.50	.57	12	10	3	3–4
A. (Lophopompilus) carolinus (Banks)	1.20	1.60	.57	12	12–14	2–3	6
A. (L.) cleora (Banks)	1.25	1.60	.50	14	20	4	——

[a]HW/HH = head width/head height, the latter measured exclusive of the labrum. ML/MW = mandibular length, measured in a straight line/mandibular width at its maximum. LS/OD = length of the longest head setae/maximum diameter of the antennal orbit.

[b]Cly. = clypeus, i.e., the number of setae forming an irregular transverse series on the anterior part, discounting a few setae which may be present near the anterior tentorial arms. Lab. = labrum. Man. = mandible. Spin. = spinneret, i.e., the number of setae to be found in a compact group close beside the spinneret on each side.

18 setae and a submarginal row of 18 pigmented sensory cones; epipharynx mostly covered with broad papillae. Mandibles 0.9 mm. long, 0.47 mm. wide at the base; sides with three small setae; ventral aspect as shown in figure 41. Maxillae and labium in poor condition, but not differing in any noticeable way from those of *thisbe*; galeae 120μ long, the maxillary palpi slightly shorter but more stout; spinneret with three setae on each side.

Genus **Hemipepsis** Dahlbom

The one larva of this genus which I have seen differs but slightly from the larva of *Pepsis*. The mandibles are somewhat broader, with the inner tooth not sharply separated from the middle tooth, and the spinneret is flanked by a group of about 14 strong setae on each side.

Hemipepsis ustulata ochroptera Stål

(Fig. 42)

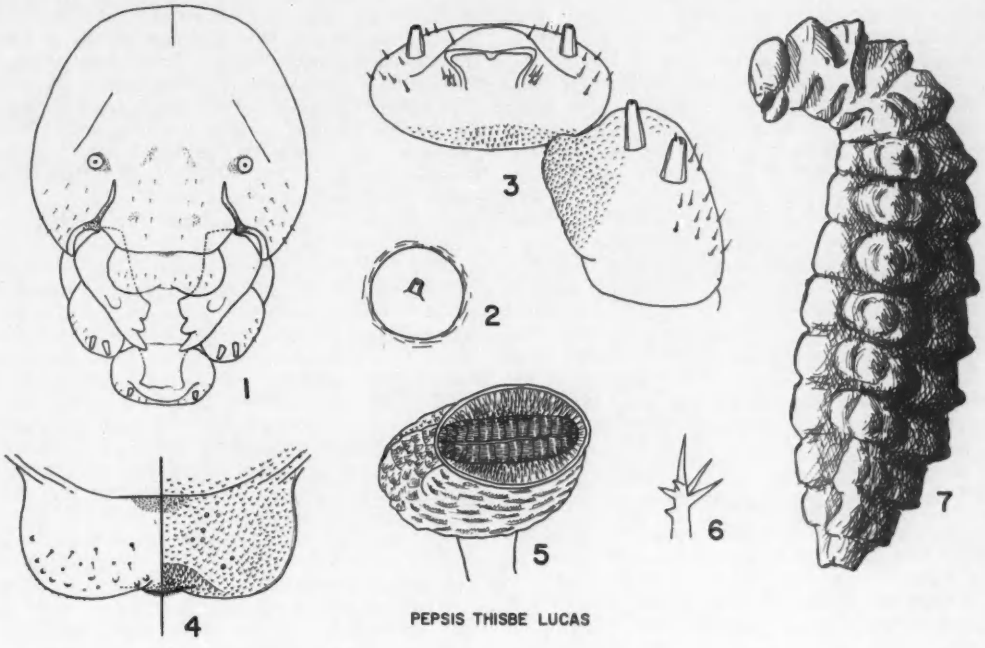
Williams (1956) has discussed the biology of this species and sent me a full-grown larva, from La Mesa, Calif., taken in the course of his studies. For some reason the head capsule of this specimen did not clear well in potash, and some of the details of head structure are obscure.

Body.—Length 22 mm.; maximum width 9 mm. Similar to that of *Pepsis thisbe*, but somewhat less strongly flattened ventrally; integument without setae, but with minute spinules on parts of the venter. Spiracles elliptical, closely resembling those of *Pepsis thisbe*.

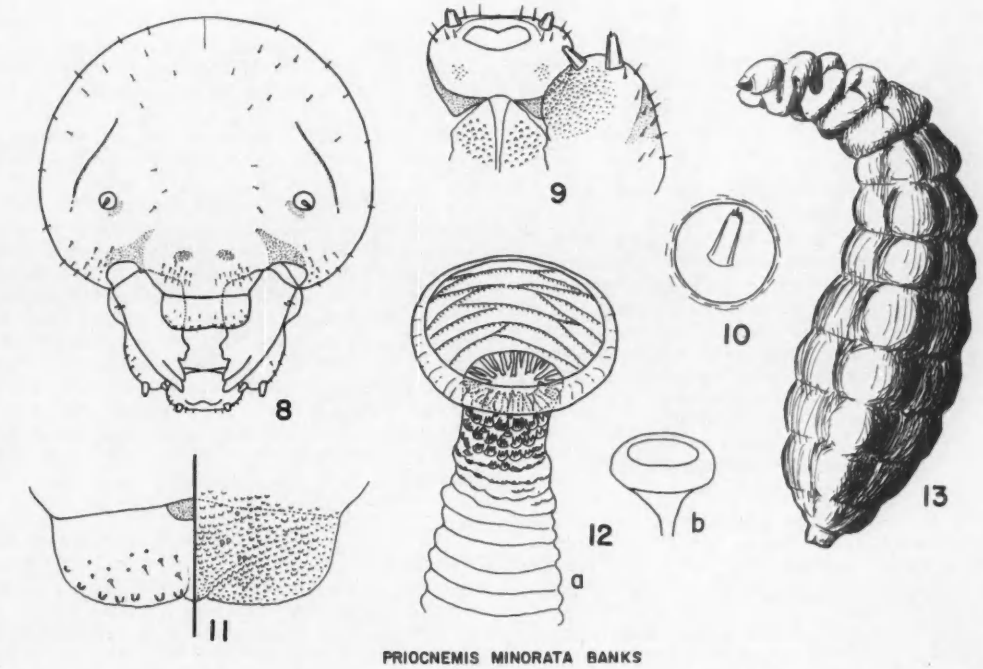
Head.—Width 2.6 mm.; height 2.25 mm.; head thus relatively broader than in *Pepsis*. Parietal bands not clearly visible in the available material,

EXPLANATION OF PLATE I

FIG. 1.—*Pepsis thisbe* Lucas, anterior view of head. FIG. 2.—Same, antenna. FIG. 3.—Same, maxilla and labium, adoral aspect. FIG. 4.—Same, labrum (left side) and epipharynx (right side). FIG. 5.—Same, anterior thoracic spiracle. FIG. 6.—Same, one of spines from lower part of spiracular atrium under high magnification. FIG. 7.—Same, body in lateral view. FIG. 8.—*Priocnemis minorata* Banks, anterior view of head. FIG. 9.—Same, maxilla and labium, adoral aspect. FIG. 10.—Same, antenna. FIG. 11.—Same, labrum (left side) and epipharynx (right side). FIG. 12.—Same, anterior thoracic spiracle (a) and second thoracic spiracle (b) drawn to same scale. FIG. 13.—Same, body in lateral view.



PEPSIS THISBE LUCAS



PRIOCNEMIS MINORATA BANKS

apparently not especially long or deeply pigmented. Antennal orbits 170μ in diameter, papillae very small, about 25μ in length and nearly as thick. Setae sparse, the longest ones measuring about 40μ. Labrum 1 mm. wide, 0.28 mm. in median height; margin of lateral lobes as well as that of the broad, truncate median lobe somewhat bristly; disc with some weak punctures but in this specimen without visible setae or sensory cones; epipharynx wholly clothed with large, sharp spinules. Mandibles 1 mm. long, 0.6 mm. in maximum width; sides with two small setae; apex with three teeth which tend to surround a strong ventral concavity, the basal tooth angular, not set off as a truncate tooth as in *Pepsis* (fig. 42). Galeae and maxillary palpi subequal in size and shape, both about 120μ long; lacinial area slightly produced, weakly spinulose. Labial palpi rather short; spinneret 0.27 mm. wide, flanked on each side by a group of about 14 strong setae.

Genus **Cryptocheilus** Panzer

I have seen no larvae of this genus, but Maneval (1936) has provided a description and figures of the European species *C. affinis* (Van der Linden). The larva of this species is unusually slender and tapers posteriorly to a slender, conical apex; the pleural lobes are strong, the spiracles small, circular, pale yellow. The head is wider than high, with long, prominent parietal bands; the antennal papillae are small but apparently more elongate than in *Pepsis*. The labrum is broad, emarginate apically, the border of the emargination microscopically crenulate; the mandibles have two apical teeth and a rounded lobe on the inner margin (fig. 43); the maxillary palpi and galeae are of about equal length, the labial palpi slightly shorter.

Genus **Priocnemis** Schiødte

In this genus the spiracles are circular and the atrial walls are only very weakly spined; the spines on the walls of the subatrium, however, appear to be of the same general type as in *Pepsis*. The antennal papillae are prominent, about half as long as the width of the orbits; the mandibles are slightly more than 1.5 times as long as their maximum width, and the inner apical tooth is broad and truncate; the spinneret has only one or two setae on each side.

Priocnemis minorata Banks

(Figs. 8–13, 44)

This description is drawn from four well-preserved larvae from Ithaca, N. Y., May-June 1953. These larvae were collected by C. M. Yoshimoto in the course of his biological studies of this species (1954).

Body.—Length 12 mm.; maximum width 3.7 mm. (fig. 13). Somewhat fusiform, more swollen toward the posterior end; pleural lobes rounded, rather strong; anal segment subtruncate, the anus situated below the middle of the segment. Prothorax bearing some minute dorsal setae; venter with minute spinules much as figured for *Dipogon* (fig. 17). Spiracles small, circular (fig. 12a) except the second thoracic spiracles very small, elliptical (fig. 12b); atrium lined with anastomosing, weakly spinose ridges; opening into subatrium lined with large spines which are often blunt or bifid apically; walls of subatrium lined with groups of spines.

Head.—Width 1.35 mm.; height 1.1 mm. (fig.8). Parietal bands of moderate length, measuring about 0.4 mm., brown in color; antennal orbits 80μ in diameter, the papillae 40μ long (fig. 10). Setae fairly numerous, the longest ones measuring 35μ; clypeus with an unusually large number of small setae (about 28). Labrum 0.4 mm. wide, bearing 12 setae and some additional punctures as well as a subapical series of 14 large, pigmented sensory cones; epipharynx covered mostly with broad, irregular spinules or papillae (fig. 11). Mandibles 0.52 mm. long, 0.31 mm. in maximum width, the sides with two small setae, the apex as shown in ventral view in fig. 44. Maxillary palpi 75μ long; galeae 60μ long; lacinial area spinulose but not notably produced; labial palpi only 23μ long; spinneret 0.14 mm. wide, with one or two small setae on each side (fig. 9).

Priocnemis cornica (Say)

(Fig. 38)

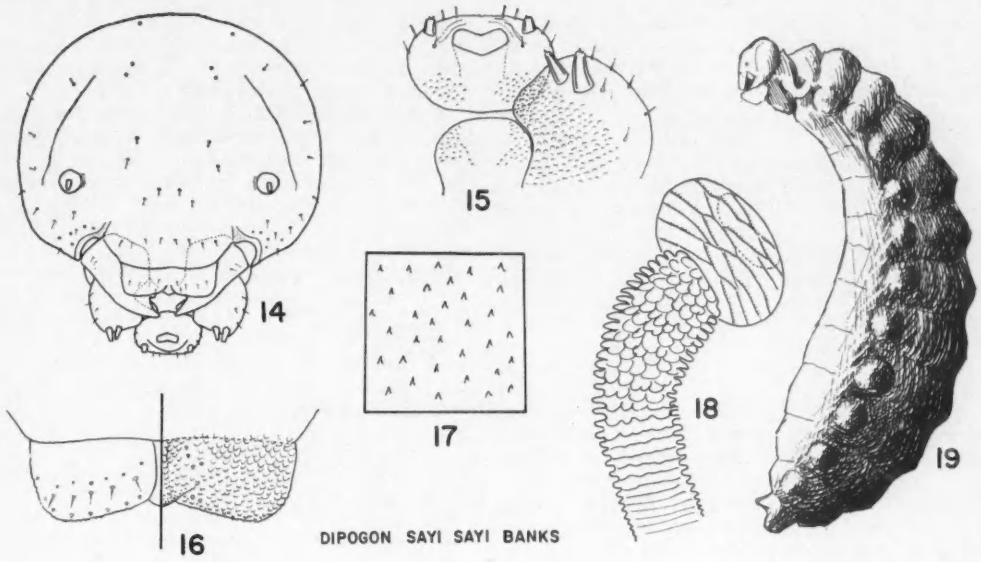
I have seen five specimens of this species, three from Ithaca, N. Y., Aug. 1953, one from Oswego Co., N. Y., July 1954, and one from Pottawatomie Co., Kansas, July 1953 (all collected by C. M. Yoshimoto).

Body.—Length 7 mm.; maximum width 1.8 mm.; in all details as described for the preceding species.

Head.—Width 0.76 mm.; height 0.68 mm.; parietal bands 0.3 mm. long; antennal orbits 60μ in diameter, the papillae 30μ long; longest head setae about 20μ long. Labrum 0.27 mm. wide, bearing 10 setae and 10 sensory cones, the median lobe slightly more strongly spinulose than in *minorata*. Mandibles 0.3 mm. long, 0.19 mm. wide at the base, as figured for *minorata* but with only a single lateral seta. Lacinial area of maxilla strongly, angularly produced; galeae and maxillary palpi both about 40μ long; labial palpi 28μ long; spinneret 90μ wide, with a single seta close beside it on each side (fig. 38).

Genus **Dipogon** Fox

The larvae of this genus live in stems, and the body is more cylindrical than in most Pompilidae; the head has a small midfrontal prominence and the anal segment is somewhat produced, both of these structures possibly serving to assist the larva in moving about in its cell. The spiracles differ from those of *Priocnemis* in lacking spines in the



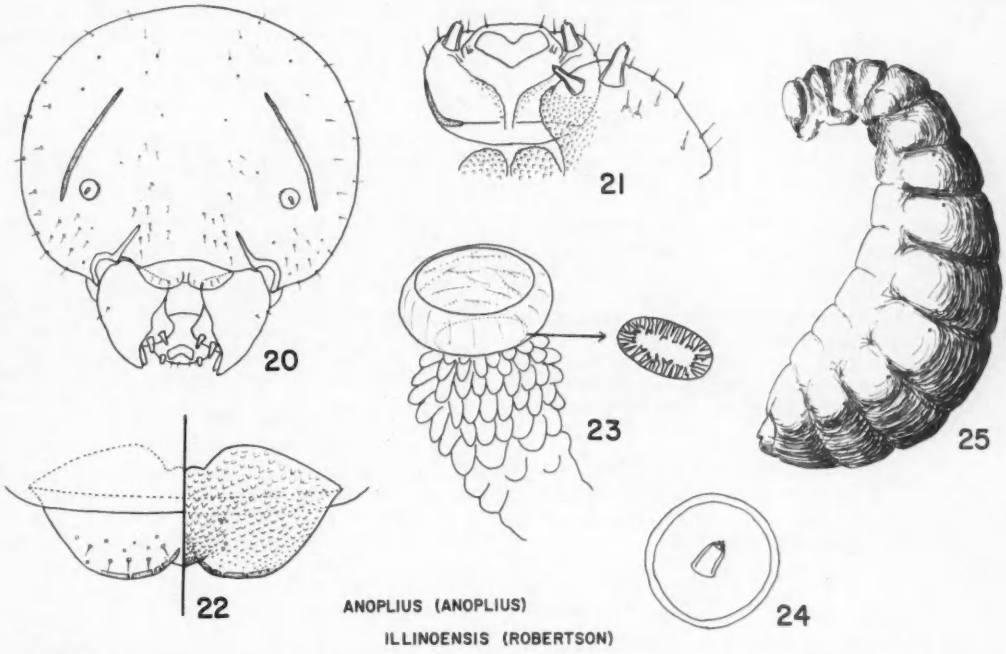


FIG. 14.—*Dipogon sayi sayi* Banks, anterior view of head. FIG. 15.—Same, maxilla and labium, adoral aspect. FIG. 16.—Same, labrum (left side) and epipharynx (right side). FIG. 17.—Same, portion of integument of prothorax under high magnification. FIG. 18.—Same, anterior thoracic spiracle. FIG. 19.—Same, body in lateral view. FIG. 20.—*Anoplius (Anoplius) illinoensis* (Robertson), anterior view of head. FIG. 21.—Same, maxilla and labium, adoral aspect. FIG. 22.—Same, labrum (left side) and epipharynx (right side). FIG. 23.—Same, anterior thoracic spiracle. FIG. 24.—Same, antenna. FIG. 25.—Same, body in lateral view.

opening between the atrium and subatrium and on the walls of the subatrium. In most other respects the resemblance to *Priocnemis* is close, but there are no setae closely flanking the spinneret.

Dipogon sayi sayi Banks
(Figs. 14–19, 45)

This species is commonly taken in wooden trap-nests in the northeastern United States; its biology recently has been discussed by Medler and Koerber (1957), who present a series of photographs of the larva feeding on a spider. I have seen eight specimens of this species, as follows: five from Ithaca, N. Y., July-Aug. 1954-56 (C. M. Yoshimoto & H. E. Evans); two from Pittsford, N. Y., Aug. 1955 (K. W. Cooper); one from Plummer's Island, Md., July 22, 1958 (K. V. Krombein).

Body.—Length 11.5 mm.; maximum width 3.5 mm. (fig. 19). Fusiform-cylindrical, slightly more thickened posteriorly than anteriorly; pleural lobes prominent; supra-anal lobe much more prominent than the subanal, both lobes somewhat protuberant. Integument with minute spinules at least over much of the thorax (fig. 17), but without noticeable setae. Spiracles circular, except the second thoracic spiracles minute, vestigial; walls of the atrium lined with weak, anastomosing ridges; walls of the subatrium thrown into innumerable small folds, but neither the subatrium nor the opening into it noticeably armed with spines (fig. 18).

Head.—Width 1.32 mm.; height 1.08 mm. (fig. 14). Parietal bands long, heavily pigmented; antennal orbits 90μ in diameter, the papillae elongate, 40μ long; longest head setae measuring about 30μ. Labrum 0.4 mm. wide, bearing 10–12 setae and 12 small sensory cones; epipharynx with about 12 sensory cones, spinulose medially and elsewhere with large papillae (fig. 16). Mandibles 0.42 mm. long, 0.27 mm. wide at the base, with two large setae on the side near the base, apically with the usual ventral concavity and three large teeth, the basal one broad and truncate (fig. 45). Maxillary palpi 100μ long; galeae 80μ long; lacinial area spinulose, the spinules grading into papillae basad; labial palpi 35μ long; spinneret 140μ wide, without setae close beside it.

Dipogon papago anomalus Dreisbach

K. V. Krombein has sent me a single specimen of this species, from Plummer's Island, Md., Sept. 9, 1956.

Body.—Length 8.5 mm.; maximum width 1.7 mm. Form much as figured for *sayi*, the anal segment similarly protuberant. Integument weakly spinulose; spiracles as figured for *sayi*.

Head.—Width 0.95 mm.; height 0.82 mm.; parietal bands 0.4 mm. long, strongly curved below; antennal orbits 75μ in diameter, the papillae 27μ long; longest setae 25μ long. Labrum 0.3 mm. wide; disc with a row of 10 setae and a subapical row of 12 sensory cones, these cones somewhat larger than in *sayi*. Mandibles 0.35 mm. long, 0.22 mm. wide at the base; form as in *sayi*, but the base with only one small seta. Maxillary palpi 60μ long; galeae more slender but about as long; lacinial area slightly projecting and clothed with small, sharp spinules; labial palpi 30μ long; spinneret 110μ wide, not noticeably emarginate medially.

Dipogon variegatus (Linnaeus)

Maneval (1939) has described the larva of this Palaearctic species. The apical abdominal segment is shown as being less protuberant than in other species of this genus, and the spiracles are not described. The resemblance to the preceding two species in most details of the head and mouthparts is striking. The head is wider than high, the parietal bands long and strongly curved below; the labrum bears numerous short setae plus a few longer ones; the lacinial area of the maxilla is produced but without sharp spinules; the mandibles, labium, and other features are about as I have described for *sayi*.

Dipogon intermedius (Dahlbom)

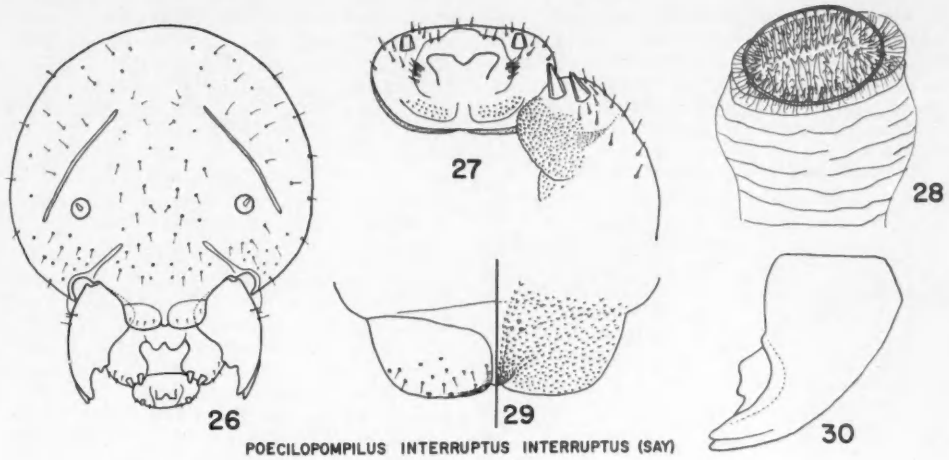
Valkeila (1955) has recently presented a brief description of the larva of this Palaearctic species. The body form is much as I have figured for *sayi*, including the protuberant anal lobes. The head is wider than high, the parietal bands long and slightly curved, the antennal papillae rather long; the labrum and mandibles are shaped as in *sayi*; the maxillae and labium are not described or figured in detail, but the galeae appear to be considerably shorter than in *sayi*.

Genus **Auplopus** Spinola

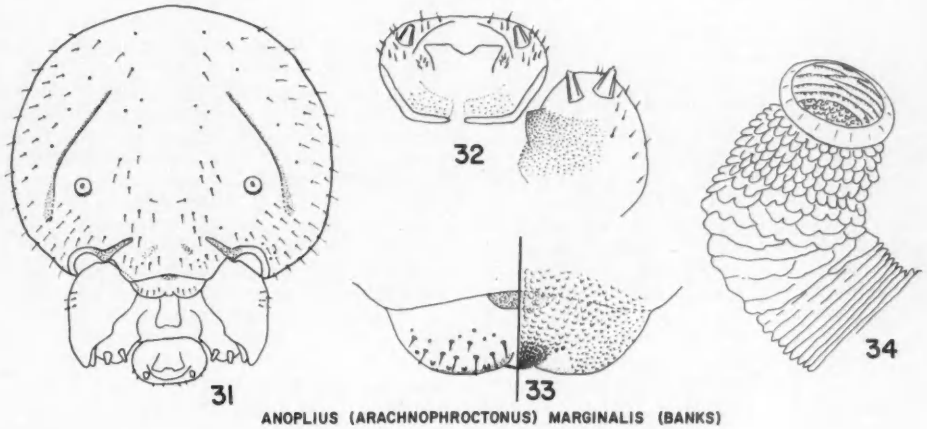
The described larvae of this genus appear to be strikingly similar to those of *Dipogon*. In part this may be a result of the fact that these larvae, like those of *Dipogon*, are adapted for life in closed cells above ground, in this case in mud

EXPLANATION OF PLATE III

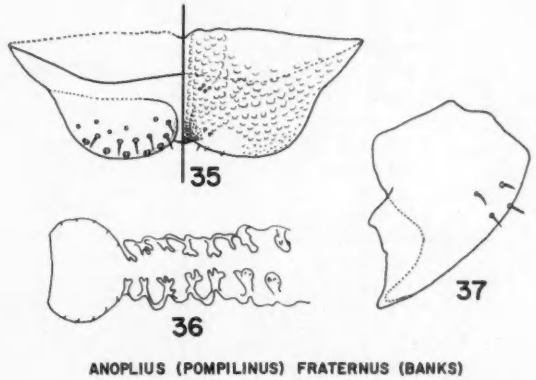
FIG. 26.—*Poecilopompilus i. interruptus* (Say), anterior view of head. FIG. 27.—Same, maxilla and labium, adoral aspect. FIG. 28.—Same, anterior thoracic spiracle. FIG. 29.—Same, labrum (left side) and epipharynx (right side). FIG. 30.—Same, mandible, ventral aspect. FIG. 31.—*Anoplius* (*Arachnophroctonus*) *marginalis* (Banks), anterior view of head. FIG. 32.—Same, maxilla and labium, adoral aspect. FIG. 33.—Same, labrum (left side) and epipharynx (right side). FIG. 34.—Same, anterior thoracic spiracle. FIG. 35.—*Anoplius* (*Pompilinus*) *fraternus* (Banks), labrum (left side) and epipharynx (right side). FIG. 36.—Same, anterior thoracic spiracle, longitudinal view. FIG. 37.—Same, mandible, dorsal aspect. FIG. 38.—*Priocnemis cornica* (Say), maxilla and labium, adoral aspect. FIG. 39.—*Anoplius* (*Pompilinus*) *marginatus* (Say), maxilla and labium, adoral aspect.



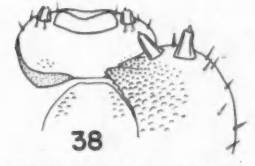
POECILOPOMPILUS INTERRUPTUS INTERRUPTUS (SAY)



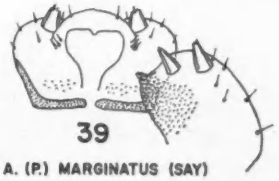
ANOPLIUS (ARACHNOPHROCTONUS) MARGINALIS (BANKS)



ANOPLIUS (POMPILINUS) FRATERNUS (BANKS)



PRIOCNEMIS CORNICA (SAY)



A. (P.) MARGINATUS (SAY)

nests. According to Grandi, the larva of *A. carbonarius* has, on each segment, a transverse series of small setae; the pleural lobes also have a few setae plus some minute, irregular ridges. These characters may prove to be characteristic of the genus *Auplopus* or the tribe Auplopodini.

Auplopus carbonarius (Scopoli)

Grandi (1926) has provided a description of the larva of this well known Palaearctic species. The body form is very much like that of *Dipogon sayi*, including the protuberant anal segment, but the supra-anal and subanal lobes are equally developed. The spiracles are not described. The head features are very much as in *Dipogon*, including long parietal bands and rather long antennal papillae. Head setae are shown as being numerous and rather long, some of them nearly as long as the diameter of the antennal orbit. The labrum has 18 large setae plus a submarginal series of small sensory cones; the margin has a strong median notch which is bristly, but apparently no well-defined median lobe. The mandibles have one lateral seta and the usual two apical teeth and one broad tooth along the inner margin. The maxillary palpi are considerably longer than the galeae; the labium has a pair of short palpi and a transverse spinneret which is concave medially. Grandi does not mention or figure any setae closely flanking the spinneret.

Auplopus ochraceus (Haupt)

Yasumatsu (1939) has described the larva of this species. The shape of the body is said to be exactly the same as in *carbonarius*. The head is similar to that species, but the setae are fewer in number and much smaller. The labrum has a distinct median lobe of small size; long setae are absent from the labrum but there are some small sensory setae. The features of the mandibles, maxillae, and labium appear to be exactly as in *carbonarius*; again, no setae are mentioned or figured close beside the spinneret.

SUBFAMILY POMPILINAE

The larvae of this subfamily which I have examined appear to lack spinules on the integument but to have a moderate number of fairly long (though inconspicuous) dorsal setae. Head setae are fairly long, in all cases at least four-tenths as long as the diameter of the antennal orbit. The mandibles of genera such as *Poecilopompilus* and *Episyron* closely resemble those of the Pepsinae, but other genera show a certain amount of reduction in the dentition. In most Pompilinae the margin of the labrum is weakly pigmented.

Genus **Poecilopompilus** Howard

The pepsine-type mandibles and elliptical spiracles (not greatly dissimilar to those of *Pepsis*) suggest that this genus may be a somewhat primitive element in the Pompilinae. In the one species in which the larva is known, there are nine setae close beside the spinneret on each side. *Batozonellus* and *Episyron* also possess numerous setae beside the spinneret and mandibles similar to those of *Poecilopompilus*. These three genera also form a closely-knit generic complex on the basis of adult characters and ethology.

Poecilopompilus interruptus interruptus (Say)
(Figs. 26–30)

This description is drawn from one specimen from Blackjack Creek, Pottawatomie Co., Kansas, June 19, 1952 (H. E. Evans), and one specimen from Kill Devil Hills, Dare Co., N. C., July 15, 1950 (K. V. Krombein) (see Krombein 1953).

Body.—Length 20 mm.; maximum width 7 mm. Abdomen very stout on the middle segments, gradually tapered anteriorly, much as figured for *Anoplius* (fig. 25); anus in the middle of the terminal segment, the supra-anal and subanal lobes not especially prominent. Integument without spinules, but the thoracic dorsum with a few setae which measure 50–70μ in length. Spiracles elliptical, the second thoracic spiracles minute; atrium lined with innumerable simple spines; opening into subatrium, as well as walls of the subatrium, lined with large, branching spines (fig. 28).

Head.—Width 2.1 mm.; height 1.85 mm. (fig. 26). Parietal bands strong, 0.9 mm. long; antennal orbits 140μ in diameter, the papillae 50μ long; setae numerous, the longest ones measuring about 95μ. Labrum 0.6 mm. wide; median lobe small; margin of lateral lobes somewhat pigmented toward the median line; disc with 16–18 setae and about 14 small setiform sensilla; epipharynx wholly clothed with small spinules (fig. 29). Mandibles 0.8 mm. long, 0.45 mm. wide at the base, the sides with two or three large setae, the apex with two sharp teeth and the inner margin with a broad, truncate tooth (fig. 30). Maxillae with dense short spinules covering the lacinial area; palpi and galeae similarly shaped and both about 80μ long; labial palpi very short, no longer than wide at the base; spinneret 0.2 mm. wide, emarginate apically, flanked on each side by a group of nine strong setae (fig. 27).

Genus **Batozonellus** Arnold

The larva of *B. lacerticida* (Pallas) was described by Grandi in 1939; in 1954 he repeated his description, with slight modification, using the same figures. The resemblance of this species to *Poecilopompilus interruptus* is great, including the elliptical spiracles. The mandibles have 4 lateral setae rather than 2 or 3, and the spinnerets are flanked by 2 groups of 12 setae rather than 9. The antennal papillae are relatively slightly shorter and the labial palpi longer than in *P. interruptus*.

Genus **Episyron** Schiødte

This genus differs from the preceding two in having circular spiracles and fewer setae on the mandibles and flanking the spinneret. The longest head setae are nearly as long as the diameter of the antennal orbit. The larvae of two species are known.

Episyron quinquenotatus quinquenotatus (Say)

(Fig. 46)

This species is described from three specimens from Ithaca, N. Y., June-Aug. 1953–54 (C. M. Yoshimoto).

Body.—Length 11 mm.; maximum width 3 mm. Form much as figured for *Anoplius* (fig. 25), but the supra-anal lobe slightly protuberant; pleural lobes relatively weak; thoracic dorsum with a few setae. Spiracles circular, the second thoracic spiracles minute; atrium lined with concentric rows of small spines; opening into subatrium armed with large, branching spines; walls of subatrium irregular.

Head.—Width 1.28 mm.; height 1.05 mm.; parietal bands long but rather pale; antennal orbits circular, 70μ in diameter; antennal papillae 25μ long; longest head setae 55μ long. Labrum 0.38 mm. wide; median lobe small; disc with 14 setae and a submarginal row of 14 small, setiform sensilla; epipharynx with minute spinules on the median lobe, elsewhere with rather broad spines which grade into papillae. Mandibles 0.44 mm. long, 0.28 mm. wide at the base; sides with a single small seta; apex with two sharp teeth and inner margin with a broad, truncate tooth (fig. 46). Maxillary palpi and galeae each about 60μ long; lacinial area slightly produced, clothed with very small spinules; labial palpi very short; spinneret 0.12 mm. wide, with a group of seven strong setae close beside it on each side.

Episyron posterus (Fox)

This description is based on a single larva collected by K. V. Krombein at Kill Devil Hills, Dare Co., N. C., June 29, 1954 (see Krombein 1955).

Body.—Length 10 mm.; maximum width 3.2 mm. Form very much as figured for *Anoplius illinoensis* (fig. 25), but the dorsum of each segment with somewhat more distinct division into two annulets; spiracles circular, the second thoracic spiracles minute; thoracic dorsum with a few small setae.

Head.—Width 1.25 mm.; height 1.0 mm.; parietal bands 0.6 mm. long; antennal orbits 75μ in diameter; antennal papillae very short, only about 20μ long; setae strong, the longest ones about 60μ long. Labrum 0.37 mm. wide; median lobe small; disc with 12 setae; apical margin lightly pigmented, with about 12 small sensilla. Mandibles and maxillae not differing notably from those of *quinquenotatus*. Labial palpi very short, no longer than broad at the base; spinneret with a group of seven strong setae close beside it on each side.

Genus **Anoplius** Dufour

I have seen larvae of 11 species of this genus, and the larva of 1 additional species has been described by Grandi. In all of these species the broad tooth on the inner margin of the mandible is not distinctly separated from the second apical tooth, the two together forming an arcuate cutting edge. The spiracles differ in structure from those of *Episyron* and *Poecilopompilus*, the labial palpi tend to be longer, and there are never more than six setae on each side of the spinneret.

The known species of this genus show differences in ratios and setal counts (see table 1) and some of them show slight differences in mandibular structure. None of these differences, however, coincide with the present division of the genus into subgenera.

Anoplius (**Anoplius**) **illinoensis** (Robertson)

(Figs. 20–25, 47)

This description is based on a single specimen collected by the writer at Ithaca, N. Y., on Sept. 23, 1956.

Body.—Length 15 mm.; maximum width 4.5 mm. (fig. 25). Much more swollen posteriorly than anteriorly; anal segment simple; pleural lobes large but not strongly protuberant; thoracic dorsum with a few setae measuring 40μ–60μ in length. Spiracles subcircular, the second thoracic spiracles minute and barely visible; atrium lined with weak, spinose ridges; opening into subatrium broadly elliptical, armed with stout spines which are mostly bified apically; subatrium with innumerable swellings, also lined in large part with spines (fig. 23).

Head.—Width 1.7 mm.; height 1.3 mm. (fig. 20). Parietal bands brown, 0.7 mm. long; antennal orbits 100μ in diameter, the papillae slender, 30μ long; setae rather short, the longest ones about 50μ long. Labrum 0.55 mm. wide, its median lobe rather small; lateral lobes with their margins weakly pigmented, a few weak sensilla set in the marginal band; disc with 10 setae plus a few punctures (fig. 22). Epipharynx with two strong sensilla on each side of the median lobe and two groups of four sensilla each basad of these; surface mostly covered with papillae which tend to be acute apically and to grade into spinules medially and latero-apically. Mandibles 0.6 mm. long, 0.37 mm. wide at the base; sides bearing two setae; apex with the second tooth continuous with a smooth cutting edge (fig. 47). Maxillae with the sides setose, the lacinial area weakly produced, spinulose; palpi and galeae both about 80μ long, the latter more slender and tapering than the former (fig. 21). Labial palpi 60μ long; spinneret 0.17 mm. wide, with two setae close beside it on each side.

Anoplius (Anoplius) virginiensis (Cresson)

This species is described from one specimen from Ithaca, N. Y. collected on July 20, 1954, by C. M. Yoshimoto.

Body.—Length 11 mm.; maximum width 3.2 mm.; form as described and figured for *illinoensis*.

Head.—Width 1.3 mm.; height 0.95 mm.; parietal bands 0.55 mm. long; antennal orbits 80μ in diameter, the papillae only 15μ long; longest head setae 40μ long. Labrum 0.45 mm. wide, very much as in *illinoensis* but the margin not noticeably pigmented. Mandibles with two strong lateral setae, shaped much as in *illinoensis*; features of maxillae and labium exactly as described for that species.

Anoplius (Anoplius) ithaca (Banks)

I have seen one specimen of this species, from Llano, Texas, July 28, 1953 (C. M. Yoshimoto). The biology has been discussed by Evans (1948).

Body.—Length 9 mm.; form much as figured for *illinoensis*, but the last abdominal segment somewhat more protuberant; spiracles circular and of much the same form as in *illinoensis*.

Head.—Width 1.2 mm.; height 0.95 mm.; parietal bands 0.5 mm. long; antennal orbits 70μ in diameter, the papillae about 20μ long; longest head setae 40μ long. Labrum 0.5 mm. wide, shaped much as in *illinoensis* but the median lobe even smaller; margin not noticeably pigmented. Features of mandibles, maxillae, and labium like those of *illinoensis* except that the spinneret has three setae close beside it on each side.

Anoplius (Pompilinus) fraternus (Banks)

(Figs. 35–37)

This description is based on two specimens taken by the writer at Flamingo, Everglades National Park, Fla., March 1954 (see Evans, Krombein, and Yoshimoto 1955).

Body.—Length 10 mm.; maximum width 3.2 mm. Form very much as in *illinoensis*, but with somewhat more numerous body setae, some setae being visible on all segments except the last. Spiracles differing from those of *illinoensis* chiefly in having fewer branched spines arming the entrance to the subatrium and the walls of the subatrium (shown in longitudinal view in fig. 36).

Head.—Width 1.4 mm.; height 1.12 mm.; parietal bands 0.6 mm. long; antennal orbits 80μ in diameter, the papillae 30μ long; setae strong, the longest ones 60μ long. Labrum 0.43 mm. wide; median lobe short, truncate; disc with an irregular row of 12 setae, also with a few punctures basad of these; margin with 10 fairly strong sensilla, weakly pigmented toward the midline (fig. 35). Epipharynx with sensilla about as in *illinoensis*; median lobe and lateral angles with minute spinules, elsewhere with broad, irregular papillae. Mandibles 0.46 mm. long, 0.35 mm. wide at the base; sides with four strong setae; basal tooth and second tooth connected by a cutting edge which has a slight basal projection and a weak notch near the middle (fig. 37). Maxillae with the lacinial area acutely produced, spinulose; galeae and palpi both about 60μ long; labium with several apical setae, including a group of three strong ones at each end of the spinneret; palpi about 40μ long.

Anoplius (Pompilinus) marginatus (Say)

(Fig. 39)

This description is based on a single specimen collected at Ithaca, N. Y., August 1954, by C. M. Yoshimoto.

Body.—Length 8 mm.; features as in the preceding species.

Head.—Width 1.1 mm.; height 0.9 mm.; length of parietal bands 0.5 mm.; width of antennal orbits 85μ, the papillae 27μ long; longest setae 33μ long. Labrum 0.36 mm. wide; disc with 12 setae; margin weakly pigmented toward the midline, with a row of 10 sensilla; epipharynx as in *fraternus*. Mandibles 0.38 mm. long, 0.26 mm. wide at the base; sides with two setae; cutting edge even, about as figured for *marginalis* (fig. 48). Maxillae and labium as shown in fig. 39; maxillary palpi 55μ long; galeae more slender, 50μ long; labial palpi 40μ long; spinneret with three setae on each side.

Anoplius (Pompilinus) subcylindricus (Banks)

This description is also based on a single specimen collected at Ithaca, N. Y., by C. M. Yoshimoto, in this case on August 11, 1953.

Body.—Length 7 mm.; essentially as described for *fraternus*.

Head.—Width 0.93 mm.; height 0.76 mm.; parietal bands 0.4 mm. long; antennal orbits 70μ in diameter, the papillae 20μ long; head setae unusually abundant, the longest ones measuring about 35μ. Labrum 0.3 mm. wide; median lobe very small; disc with 12 setae plus some punctures; margin weakly pigmented, with 8 sensilla; epipharynx as figured for *fraternus*. Mandibles 0.33 mm. long, 0.21 mm. wide at the base; sides with three setae; cutting edge about as in *marginalis* (fig. 48). Maxillae and labium much as figured for *marginatus* (fig. 39); lacinial area acutely produced, spinulose; maxillary palpi 45μ long; galeae 40μ long; labial palpi 30μ long; spinneret flanked by three setae on each side.

Anoplius (Pompilinus) krombeini Evans

I have seen two specimens of this species, both taken on March 30, 1954, at Olga, Lee Co., Fla. (C. M. Yoshimoto & H. E. Evans).

Body.—Length 8 mm.; form as described for *fraternus*.

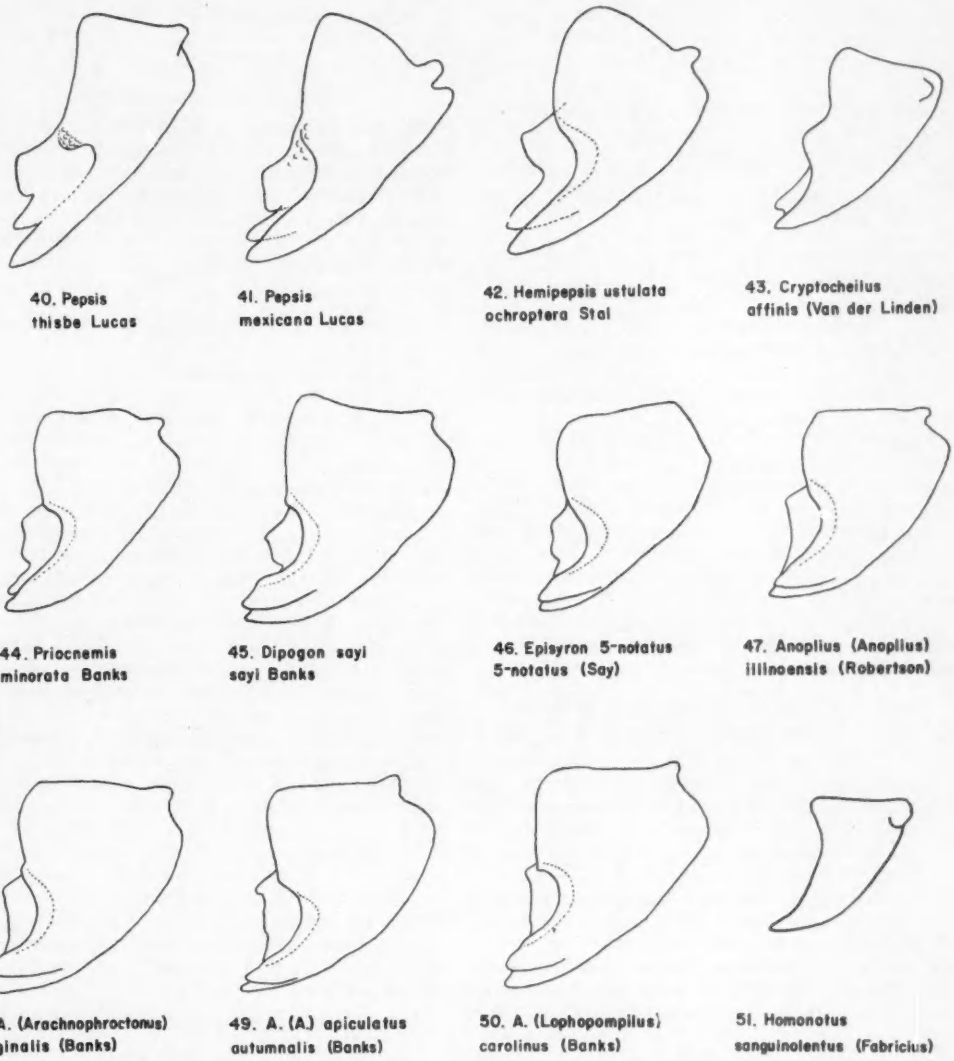
Head.—Width 1.1 mm.; height 0.95 mm.; length of parietal bands 0.45 mm.; width of antennal orbits 70μ; length of antennal papillae 25μ;

longest setae measuring 35μ. Labrum 0.33 mm. wide; disc with 10 setae plus some punctures; margin slightly pigmented, with 10 sensilla. Mandibles 0.34 mm. long, 0.23 mm. wide at the base; sides with two setae; apex as in the preceding two species. Maxillary palpi stout, 50μ long; galeae more slender and tapering, also 50μ long; lacinial area spinulose, somewhat produced apically. Labial palpi 40μ long; spinneret flanked by the usual group of three setae on each side.

Anoplius (Arachnophroctonus) marginalis (Banks)
(Figs. 31–34, 48)

This description is drawn from a single specimen from Reno Co., Kansas, July 7, 1953 (H. E. Evans & C. M. Yoshimoto).

Body.—Length 20 mm.; maximum width 7 mm. Form essentially as figured for *illinoensis*; dorsal setae inconspicuous, apparently confined to the thorax. Spiracles circular, except the second thoracic spiracles minute, slit-like; atrium shallow,


40. Pepsis thisbe Lucas
41. Pepsis mexicana Lucas
42. Hemipepsis ustulata ochroptera Stal
43. Cryptocheilus affinis (Van der Linden)
44. Priocnemis minorata Banks
45. Dipogon sayi sayi Banks
46. Episyron 5-notatus 5-notatus (Say)
47. Anoplius (Anoplius) illinoensis (Robertson)
48. A. (Arachnophroctonus) marginalis (Banks)
49. A. (A.) apiculatus autumnalis (Banks)
50. A. (Lophopompilus) carolinus (Banks)
51. Homonotus sanguinolentus (Fabricius)

FIGS. 40–51.—Mandibles of various species of Pompilidae, ventral aspect. Figures 43 and 51 are redrawn after Maneval 1936; all others original.

lined with spinose ridges; subatrium lined with short, blunt spines (fig. 34).

Head.—Width 2.4 mm.; height 1.95 mm. (fig. 31). Parietal bands prominent, 1.1 mm. long; antennal orbits 120μ in diameter, the papillae very short, only about 23μ long; head setae numerous, the longest ones about 100μ long. Labrum 0.8 mm. wide; median lobe fairly strong, spinulose; apical margin of lateral lobes narrowly pigmented, each lobe with six sensory cones and with nine setae and seven nonsetigerous punctures; epipharynx with small spinules which grade into large papillae medio-basally (fig. 33). Mandibles 0.82 mm. long, 0.51 mm. wide at the base; sides with four or five setae; cutting edge evenly arched (fig. 48). Maxillary palpi 75μ long; galeae slender, 85μ long; lacinial area spinulose, with an angular lobe; labial palpi 70μ long; spinneret with a group of five small setae on each side.

Anoplius (Arachnophroctonus) semirufus (Cresson)

I have seen two specimens of this species, both from Kill Devil Hills, Dare Co. N. C., July 17–18, 1950 (K. V. Krombein) (see Krombein 1953).

Body.—Length 8 mm.; maximum width 2.3 mm.; features as in the preceding species. Spiracles much as figured for *illinoensis*, the spines lining the walls of the subatrium long and mostly branched apically.

Head.—Width 1.25 mm.; height 0.95 mm.; parietal bands 0.4 mm. long; antennal orbits 80μ in diameter, the papillae 22μ long; longest setae 45μ long. Labrum 0.38 mm. wide, similar to that of *marginalis* but with only 10 setae. Mandibles 0.4 mm. long, 0.25 mm. wide at the base; sides with two strong setae; apical teeth as figured for *marginalis* (fig. 48). Maxillae with the galeae slightly longer than the palpi, the lacinial area with an angular, projecting lobe; spinneret with only three setae on each side.

Anoplius (Arachnophroctonus) apiculatus autumnalis (Banks)

(Fig. 49)

This description is based on five specimens from Blackjack Creek, Pottawatomie Co., Kansas, collected in July 1952 in connection with biological studies which have since been published (Evans, Lin, and Yoshimoto 1953).

Body.—Length 13 mm.; maximum width 4 mm.; form essentially as figured for *illinoensis*; dorsum of each segment except the last with a few small setae, those on the anterior three segments larger than the others. Spiracles small, the second thoracic spiracles minute, slit-like; walls of the atrium lined with anastomosing, weakly spinose ridges; walls of the subatrium thrown into innumerable small folds which internally form spinose projections.

Head.—Width 1.55 mm.; height 1.22 mm.; parietal bands 0.6 mm. long; antennal orbits 70μ in diameter, the papillae 30μ long; setae rather sparse, the longest ones measuring 40μ. Labrum 0.48 mm. wide, much like that of *marginalis* but the margin very weakly if at all pigmented, the disc with only 10 setae; epipharynx with dense spinules on the median lobe, elsewhere with broad papillae with spinose edges. Mandibles 0.5 mm. long, 0.33 mm. wide; sides with three setae; basal end of cutting edge produced as a small tooth (fig. 49). Maxillary palpi and galeae both about 60μ long; lacinial area slightly, roundly protuberant, spinulose; labial palpi 45μ long; spinneret flanked by a group of three or four setae on each side.

Anoplius (Arachnophroctonus) apiculatus pretiosus (Banks)

The two available larvae of this subspecies are strikingly similar to those of the preceding form; this includes the unusual shape of the cutting edge of the mandibles as well as other features. One of these larvae is from Kill Devil Hills, Dare Co., N. C., July 17, 1950 (K. V. Krombein (see Krombein 1953), the other from Marco Beach, Fla., March 28, 1954 (C. M. Yoshimoto).

Anoplius (Lophopompilus) carolinus (Banks)

(Fig. 50)

This description is based on three specimens collected by C. M. Yoshimoto at Six-mile Creek, Ithaca, N. Y., during August 1953.

Body.—Length 14 mm.; maximum width 5 mm.; form much as figured for *illinoensis*, but the supra-anal and subanal lobes slightly more protuberant; setae on dorsum very minute and inconspicuous. First thoracic spiracles circular-elliptical, slightly larger than the abdominal spiracles; second thoracic spiracles minute, slit-like; spiracular structure not differing noticeably from that of *marginalis* (fig. 34).

Head.—Width 1.72 mm.; height 1.48 mm.; parietal bands 0.7 mm. long; antennal orbits 80μ in diameter, the papillae 30μ long; longest head setae measuring about 45μ. Labrum 0.6 mm. wide, 0.15 mm. in median height; median lobe subacute; margins of lateral lobes weakly pigmented, each lobe with six marginal sensory cones and six or seven discal setae; features of epipharynx very much as figured for *fraternus* (fig. 35). Mandibles 0.6 mm. long, 0.37 mm. wide at the base; side with two or three setae; apex as shown in figure 50. Maxillary palpi and galeae both about 80μ long; lacinial area densely spinulose, weakly, roundly protuberant; labial palpi 60μ long; spinneret with six setae in a compact group on each side.

Anoplius (Lophopompilus) cleora (Banks)

The single available larva of this species does not appear to be fully grown, and I suspect it is in the penultimate instar. This larva is from Blackjack Creek, Pottawatomie Co., Kansas, Aug. 13, 1952 (C. M. Yoshimoto).

Body.—Length about 10 mm.; features as described for *carolinus*.

Head.—Width 1.55 mm.; height 1.25 mm.; parietal bands 0.6 mm. long; antennal orbits 80μ in diameter, the papillae 30μ long; longest head setae measuring about 40μ. Labrum 0.55 mm. wide; apical margin pigmented, with 10 sensory cones; disc with about 20 setae; epipharynx with spinules which are much more acute than in *carolinus*. Mandibles 0.57 mm. long, 0.36 mm. wide at the base; sides with four setae; inner end of cutting edge weakly produced, as figured for *carolinus* (fig. 50). Maxillary palpi and galeae both about 75μ long; labial palpi 60μ long; spinneret 0.17 mm. wide, emarginate apically.

Anoplius atricolor Móczár

The larva of this Palaearctic species has recently been described by Grandi (1954). The antennal papillae are rather long, the head setae also long. The median lobe of the labrum is not well developed; the epipharynx is covered with broad papillae; the mandibles are shaped much as in *apiculatus autumnalis*, and have four lateral setae. The galeae and maxillary palpi are subequal in length, the lacinial area roundly protuberant; the spinneret is concave apically.

Genus **Homonotus** Dahlbom

The larva of *H. sanguinolentus* (Fabricius) has been described by Maneval (1936). This larva is so different from that of other Pompilidae that I present below a free translation of Maneval's entire description. *Homonotus* is highly specialized in adult structure and the larvae develop as ectoparasites of spiders of the genus *Cheiracanthium*, so it is not surprising that the larvae exhibit many unusual features.

Homonotus sanguinolentus (Fabricius)

(Fig. 51)

Body.—Length when extended 10.5 mm.; maximum dorsal width 4.5 mm.; somewhat drawn out into a neck anteriorly and moderately attenuate posteriorly, translucent, slightly violescent except the head, which is opaline; entirely glabrous, with the integument microscopically transversely striolate. Head sharply set off, the segments which follow it more slender than those farther back; intersegmentary lines well marked; pleural lobes projecting.

Head.—Seen in profile, strongly prognathous, the epicranium evenly convex; seen from in front, wholly covered with short setae which are directed forward, the antennae prominent, fairly long. Labrum sclerotized, especially its anterior margin, emarginate medially, separated from the clypeus by a suture, provided with several tactile setae. Mandibles strongly sclerotized, reddish-brown, thickened at the base, abruptly narrowed apically to a subacute point, provided at their base externally with a blunt process (fig. 51). Maxillae thick, truncate; palpi located at the distal external angle, slightly larger than the galeae. Labium twice as wide as long, rounded behind and on the sides; labial palpi slightly smaller than the maxillary palpi; spinneret appearing in the form of a weak crease, tubes very small and hardly projecting.

DISCUSSION

The larvae of all aculeate Hymenoptera other than Pompilidae have, as far as I know, 10 pairs of well developed spiracles. The vestigial second thoracic spiracles of the Pompilidae should, therefore, provide a useful character for distinguishing the larvae of this family. Other characters useful on the family level include the presence of parietal bands and antennal papillae, the trilobed labrum (not described for *Homonotus* and a very few other forms), the tridentate mandibles having the basal tooth broad and blunt (some exceptions as noted in text), and the rather narrow spinneret which is more prominent laterally than medially.

Unfortunately no larvae are known for any of the Ceropalinae, and these may differ widely from other Pompilidae. The two major subfamilies, the Pompilinae and the Pepsinae, seem to differ only on minor characters if at all. It is disconcerting, though not surprising, to be unable to support this subfamilial separation on larval characters. There are no known ethological differences between the two groups, and the adult structural differences break down in some genera. I have long been convinced that there are only two groups of Pompilidae deserving of subfamily status, the Ceropalinae (including only *Ceropales*, *Xanthampulex*, and *Irenangelus*) and the Pompilinae (including all other Pompilidae). At this stage I can hardly say that this is supported by larval characters, but at least it is not contradicted. On larval characters, one might place *Homonotus* in a separate subfamily, but adult structure suggests that this is only a specialized pompiline.

That larval characters are by no means useless is shown by the fact that certain generic complexes do hold together on larval structure as they do on adult structure. For example, the genera *Poecilopompilus*, *Batozonellus*, and *Episyron* have very similar larvae, all with numerous setae in a close group on each side of the spinneret. These genera also stand together on adult structure and on ethology (for example, all use Epeiridae as prey). The genus *Anoplius*, used in a broad sense to include as subgenera several groups often ranked as full genera, holds together nicely by virtue of the characteristic mandibles.

It is difficult to point to any clear-cut phylogenetic trends in pompilid larvae at this time. The mandibles are, however, suggestive (figs. 40–51). I suspect that the rather elongate mandibles of *Pepsis*, with a weak ventral concavity and

the three teeth in nearly the same plane, may be as primitive as any. In most Pompilidae the ventral concavity is strong and the teeth tend to surround it. Reduction in the teeth is shown to some degree in *Anoplius* and at its ultimate in *Homonotus*. Of the genera of Pompilini studied, certainly *Poecilopompilus* is as primitive as any, for the mandibles are unspecialized and the spiracles elliptical and suggestive of those of *Pepsis*.

On the whole, I feel that the study of pompilid larvae is off to a promising beginning and that eventually larval characters may prove of much value in helping to classify this notoriously difficult family. The family Pompilidae is much more homogeneous than the Sphecidae, and one does not find the striking differences in larval structure which occur in that family. Nevertheless differences do occur, and every effort should be made to collect and describe the larvae of additional species and genera.

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CLASSIFICATION OF THE PSYCHODINI (PSYCHODIDAE: DIPTERA)[1]

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ABSTRACT

This tribe of the Psychodidae is defined and classified, with keys to and descriptions of six genera. The structure of the labellum is employed for the first time in classification, and other characters of the male and female genitalia, the wings, and the head are considered. It is postulated that the tribe arose from a *Brunettia*-like ancestor, that one line of development led to *Trichopsychoda* and possibly to *Lepidopsychoda*, and that the main phylogenetic line gave rise to *Philosepedon*, *Threticus*, *Psychoda*, and the new genus **Eurygarka** (type, *Psychoda helicis* Dyar 1929). Species assigned to each genus (except *Psychoda*) are listed, with bibliography and distribution for each species. Other new generic reassignments include 1 species to *Trichopsychoda*, 11 to *Philosepedon*, and 7 to *Threticus*.

The present study is an attempt to classify members of the tribe Psychodini based on a re-study of available characters and re-evaluation of the various groups. The tribe belongs to the subfamily Psychodinae and is, in general, composed of small gray or yellowish species belonging to the genus *Psychoda* and allied groups.

Eaton (1904) erected the subgenera *Philosepedon*, *Threticus*, and *Logima* within the genus *Psychoda* based on the shortened surstyle and multiple tenacula of the male genitalia and the presence of erect hairs on R_1. Tonnoir (1922) recognized the group *Trichopsychoda* as another subgenus of *Psychoda* distinguished by the presence of vestiture on the wing membrane. *Lepidopsychoda* was described by Edwards (1928) to receive a species allied to species of *Psychoda* with scales on the wing membrane.

The above groups were placed in the tribe Psychodini and subtribe Psychodina by Enderlein (1937). In the same subtribe were included

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other genera related to *Pericoma*. *Philosepedon*, *Threticus*, and *Logima* were treated as subgenera of *Psychoda*. *Trichopsychoda* was accorded full generic status and *Lepidopsychoda* was omitted. Subsequent authors (Tonnoir 1940, Jung 1956) have treated *Philosepedon* and *Threticus* as subgenera of *Psychoda*, *Logima* a synonym of *Psychoda*, and *Trichopsychoda* a full genus.

Previous workers have not considered the structure of the labellum in their classification of the genus *Psychoda* and related groups. Yet this structure seems to be of basic taxonomic importance and one of the most important keys to the classification of the Psychodini. In all psychodids, except the Phlebotominae and *Psychoda*, the labellum is a fleshy, bulbous structure flattened on the apex (fig. 3). The stability of the bulbous labellum, as shown by its extensive distribution in the various groups of the family, has led to the conclusion that the change from the primitive condition was a major one, not easily achieved, and worthy of serious taxonomic consideration. To be sure, other characters must be used in constructing a classification. The male genitalia are especially important and also useful are the antennal sensory filaments, shape of the head, female genitalia, etc., but the labellum seems the most critical single character in determining the relationships of other groups to the dominant genus *Psychoda*, s.s., and is a character not used previously..

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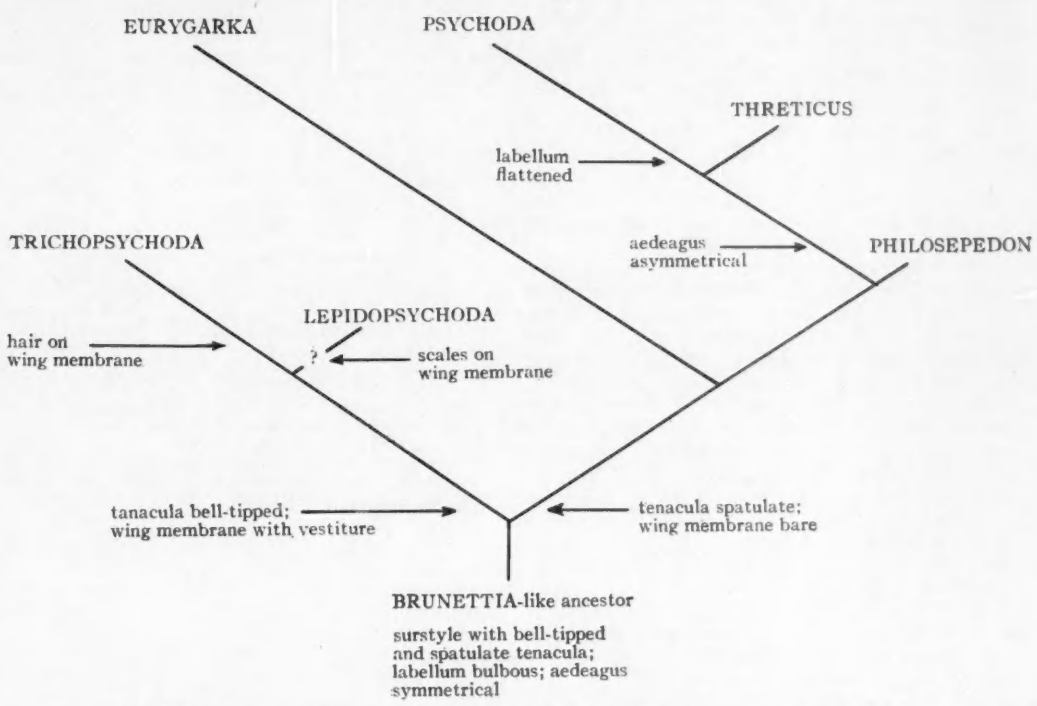

FIG. 1.—Diagrammatic representation of origin and relationships of the tribe Psychodini, showing some important morphological changes.

PHYLOGENETIC RELATIONSHIPS

The genus *Trichopsychoda* is perhaps the closest to being an annectant group between the Psychodini and its nearest psychodid relative. It has male genitalia much like those of *Brunettia*, with short surstyli which bear multiple, bell-shaped tenacula. The wing venation, head, antennae, and sensory filaments are like those of other Psychodini. It also has distinctive features of its own in the hairy membrane and incomplete forks of the wing. Thus *Trichopsychoda* is in the anomalous position of possessing characters of two genera plus features of its own, but is clearly most closely related to the Psychodini. While it indicates derivation of the Psychodini from a

Brunettia-like form (as already pointed out by Satchell 1955: 49), it is quite far removed from the ancestor of the group.

It is quite possible that the Psychodini were derived from a primitive *Brunettia*-like form that had both bell-tipped and spatulate tenacula (fig. 1). A number of species of *Brunettia* possess this feature, such as *B. splendens* Tonn., from Africa, *biformis* Edwards from Polynesia, and others. Perhaps the primitive psychodine ancestor had these combined genitalic features and early in the history of the group there was a split. One branch lost the spatulate tenacula and gave rise to *Trichopsychoda* (and also possibly *Lepidopsychoda*, but not enough details are available about this genus to be certain of its relationships). The other branch, the most productive, lost the bell-tipped tenacula and gave rise to the other genera of the Psychodini.

The genus *Eurygarka* is markedly divergent from the other psychodines in the structure of the female genitalia and antennal sensory filaments. At present it stands rather by itself as a monotypic genus and presumably arose from the second main branch of the tribe.

Philosepedon, *Threticus* and *Psychoda* are three closely related genera. *Philosepedon* is the least specialized of the three in having a bulbous labellum, 16-segmented antennae with the three reduced, terminal segments present, Y-shaped antennal sensory filaments, and symmetrical aedeagus of the male genitalia. The distinguishing features of *Threticus* and *Psychoda* can be derived from those of *Philosepedon* and those genera probably arose from the ancestral stock of *Philosepedon*.

Loss of the right lateral shaft of the aedeagus of a *Philosepedon*-like form might have been the first step toward the evolution of *Threticus* and *Psychoda*. The loss of one of the anterior branches of the antennal sensory filaments would give rise to the species now placed in the genus *Threticus*; modification of the labellum would lead to the genus *Psychoda*.

The changes that occurred when the labellum changed to the flattened structure of *Psychoda* seem to have had great significance in the evolution of the group, for this genus contains the bulk of psychodine species and gives the tribe its dominant position alongside the other major groups of Psychodidae. The bulk of the species of Psychodini are those with the flattened labellum of the genus *Psychoda* and, judged on the basis of number of species, far and away the most successful genus of the tribe.

That the above conclusions are tentatively advanced should be obvious, but at least it is a start. At a later date it will be possible to corroborate, modify or abandon the above scheme as more complete information regarding immature stages, biology, zoogeography, etc. becomes available.

Tribe **Psychodini**

Adult.—Small to medium-sized, wing length 1 to 3 mm.; vestiture usually uniformly pale yellow or gray in color, spotted in few species. Antenna with 14 to 16 segments, longer than width of wing; verticils well developed, cupuliform; sensory filaments generally Y-shaped and longer than segment bearing them; flagellar segments nodiform; terminal segments beyond 13 always reduced in size. Wing with acute apex, radial fork distad of medial, R_5 ending exactly at apex.

KEY TO GENERA OF PSYCHODINI

1. Wing membrane with vestiture 2
   Wing membrane without vestiture 4
2. Wing vestiture consisting of hairs 3
   Wing vestiture consisting of scales ... **Lepidopsychoda**
3. Vein bifurcations R_{2+3} and M_{1+2} always absent at base, thus forks incomplete ..... **Trichopsychoda**
   Bifurcations complete, or only one incomplete ..... **Philosepedon,** *pars*
4. Sensory filaments unbranched elements or without posterior branch 5
   Sensory filaments of antenna Y-shaped (sometimes 3 anterior branches) 6
5. Sensory filaments single, consisting of a sinuate branch ..... **Threticus**
   Sensory filaments consisting of a pair of broad, leaf-like anterior branches ..... **Eurygarka**
6. Labellum bulbous (fig. 3); antenna with 16 segments ..... **Philosepedon**
   Labellum flattened (fig. 2); antenna with 14 to 16 segments ..... **Psychoda**

Genus **Trichopsychoda** Tonnoir

Trichopsychoda Tonnoir, 1922, Ann. Soc. Ent. Belg. 62: 59 (subgenus of *Psychoda*); Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 87; Freeman, 1950, Hndbk. Ident. Brit. Ins. 9(2): 80, 91; Satchell, 1953, Austral. Jour. Zool. 1: 391; 1955, Proc. Roy. Ent. Soc. London (B) 24: 50; Quate, 1959, Insects Micronesia, Bishop Mus. Vol. 12, No. 4, in press.

Adult.—Head: vertex longer than width of eye bridge; eye bridge (median projection of eyes above antenna) with four rows of facets. Labellum bulbous, apically with bristles, but without teeth; palpus about as long as head from posterior margin to apex of mouth parts, first palpal segment more than one-half length of third segment. Antenna almost always with 16 segments (15 in *montana* Satchell), terminal segments beyond 13 reduced, separated; sensory filaments Y-shaped.

Wing with forks incomplete; base of R_3 distad of base of M_2; R_5 ending at apex; membrane densely covered with hairs.

Male genitalia: surstyle small, tenacula long and slender, with number of bell-shaped tips; aedeagus symmetrical.

Female genitalia: genital digit absent; subgenital plate bilobed or only with apical concavity; spermatheca large. Cerci moderately slender, longer than subgenital plate.

Type species: *Psychoda hirtella* Tonnoir (by original designation).

Distribution: in all zoogeographical regions except Neotropical.

Satchell (1955) reviewed the genus *Trichopsychoda* and broadened it to include all the species of the Psychodini with hairs on the membrane. I do not agree with this generic diagnosis and believe that Satchell includes in the genus a number of species which are not congeneric with *T. hirtella*, the type species, but properly belong to the genus *Philosepedon*.

The hairy-winged species removed from *Trichopsychoda* do not possess the genitalic characters of this genus, nor are the bases of R_3 and M_2 absent. Removing these species, there is left a nucleus of closely related species well separated from the other Psychodini on conspicuous features of wing and genitalic structures, namely the hairy membrane, atrophied vein bifurcations, the *Brunettia*-like male surstyle, and the characteristic female genitalia (not easily defined in words, but evident in available illustrations).

Distribution: Great Britain and western Europe.

Trichopsychoda insulicola (Quate)
new combination

Psychoda insulicola Quate, 1954, Proc. Hawaiian Ent. Soc. 15: 342; 1955, Univ. Calif. Publ. Ent. 10: 225.

Distribution: southeastern United States, Hawaii.

Trichopsychoda montana Satchell

Trichopsychoda montana Satchell, 1953, Austral. Jour. Zool. 1: 391.

Distribution: Australia.

Genus **Lepidopsychoda** Edwards

Lepidopsychoda Edwards, 1928, Ins. Samoa, Brit. Mus. (Nat. Hist.), Pt. 6, p. 71; Fairchild, 1951, Bull. Brooklyn Ent. Soc. 46: 14.

Type species: *Lepidopsychoda tineiformis* Edwards (by original designation).

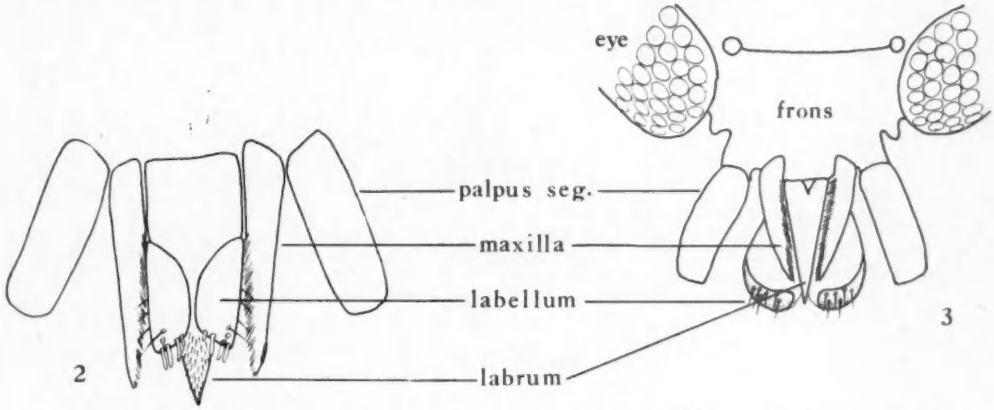

FIG. 2.—Mouth parts and anterior part of head of *Threticus bicolor* showing bulbous labellum, dorsal view.
FIG. 3.—Mouth parts of *Psychoda alternata* showing flattened labellum, ventral view.

INCLUDED SPECIES

Trichopsychoda africana Satchell

Trichopsychoda africana Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 51.

Distribution: Africa (Natal).

Trichopsychoda boninensis Quate

Trichopsychoda boninensis Quate, 1959, Insects Micronesia, Bishop Mus. Vol. 12, No. 4, in press.

Distribution: Bonin Isl.

Trichopsychoda carolinensis Quate

Trichopsychoda carolinensis Quate, 1959, Insects Micronesia, Bishop Mus. Vol. 12, No. 4, in press.

Distribution: central Caroline Isl.

Trichopsychoda hirtella (Tonnoir)

Psychoda hirtella Tonnoir, 1919, Ann. Soc. Ent. Belg. 59: 15.

Psychoda (*Trichopsychoda*) *hirtella*, Tonnoir, 1922, Ann. Soc. Ent. Belg. 62: 60; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 87.

Trichopsychoda hirtella, Edwards, *in* Tonnoir, 1940, Trans. Soc. Brit. Ent. 7: 61; Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 50.

According to Edwards (1928) and Satchell (in. litt.), *Lepidopsychoda* is related to *Psychoda* but differs in that the wing is covered with scales instead of hairs. The antennae are 16-segmented, with the terminal three segments reduced and separated, R_5 ends exactly at the wing tip, and the elongate male surstyle bears two tenacula. While I have not seen specimens of this genus, I would assume that the mouth parts are bulbous, as it appears most closely related to *Trichopsychoda* in which this condition exists.

Distribution: Oriental.

INCLUDED SPECIES

Lepidopsychoda tineiformis Edwards

Lepidopsychoda tineiformis Edwards, 1928, Ins. Samoa, Brit. Mus. (Nat. Hist.), Pt. 6, p. 72; Satchell, 1950, Proc. Roy. Ent. Soc. London (B) 19: 184, 1953, ibid., 22: 188.

Distribution: Samoa, Fiji.

Lepidopsychoda trimicra (Edwards)

Brunettia (*Parabrunettia*) *trimicra* Edwards, 1927, Treubia, 9: 364; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 105.

Lepidopsychoda trimicra, Edwards, 1928, Ins. Samoa, Brit. Mus. (Nat. Hist.), Pt. 6, p. 72.

Distribution: Java.

Genus **Philosepedon** Eaton

Philosepedon Eaton, 1904, Ent. Mo. Mag. (2) 15: 57; 1913, Trans. Linn. Soc. London (2) 15: 429; Tonnoir, 1922, Ann. Soc. Ent. Belg., 62: 61 (subgenus); Enderlein, 1935, Sitz. Gesell. Natur. Freunde 1935: 248; 1936, Tier. Mitteleur. 6 (Abt. 16): 29; 1937, Deutsche Ent. Zeitschr. 1936: 87; Tonnoir, 1940, Trans. Soc. Brit. Ent. 7: 32 (subgenus); Jung, 1956, Deutsche Ent. Zeitschr. (n.F.) 3: 190 (subgenus) (gender feminine).

stocky, not much longer than 9th tergite, generally bearing two or three tenacula, but some species with only one; aedeagus (fig. 4) approximately symmetrical, consisting of central, main shaft and one or two pairs of shorter, flanking spines or rods.

Female genitalia: genital digit absent. Cerci (ovipositor) equal to or shorter than subgenital plate, generally shorter than *Psychoda* s.s.

Type species: *Psychoda humeralis* Meigen (by original designation, monotypic).

Distribution: Holarctic and Ethiopian.

As originally defined on the basis of two tenacula of the male surstyle and used by subsequent authors (Tonnoir 1922, 1940; Jung 1956)

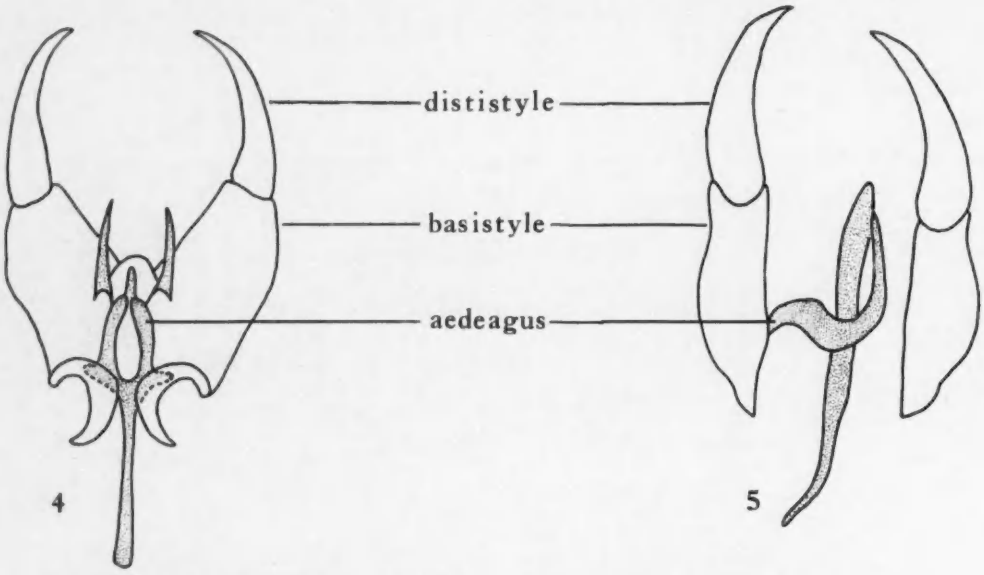

FIG. 4.—*Philosepedon humeralis*, coxites and aedeagus, showing symmetrical aedeagus.
FIG. 5.—*Psychoda pusilla*, coxites and aedeagus, showing asymmetrical aedeagus.

Adult.—Head: vertex long, two or three times as long as width of eye bridge; eye bridge with three or four rows of facets. Labellum bulbous, apically with bristles, but without teeth; palpus long, longer than entire length of head from posterior margin to apex of mouth parts, first palpal segment short, one-half or less length of third and fourth segments. Antenna with 16 segments, terminal 3 reduced and almost always clearly separated; sensory filaments Y-shaped.

Wing rather narrow; fork R_{2+3} distad of M_{1+2} by distance equal to more than three times width of cell R_2 at point of bifurcation; forks generally complete; R_5 ending at wing apex; membrane usually without vestiture.

Male genitalia: surstyle usually short and

this group was not based on solid foundations and sometimes was ignored (Freeman 1950). In my opinion the fundamental differences between the mouth parts of this group and those of *Psychoda* cannot be ignored and necessitate its recognition as a separate group. Combined with the characters mentioned in the above description, the mouth parts substantiate the belief that the group is a valid genus.

INCLUDED SPECIES

The following species belong to the genus *Philosepedon*. Undoubtedly additional species also belong, but a description of the labellum is lacking from most works and this prevents definite placement of the species.

Philosepedon bishoppi (del Rosario) new combination

Psychoda bishoppi del Rosario, 1936, Philip. Jour. Sci. 59: 141; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 205; Quate, 1955, Univ. Calif. Publ. Ent. 10: 230.

Distribution: eastern United States.

Philosepedon distyla (Quate), new combination

Psychoda distyla Quate, 1957, Nat. Malgache 9: 259.

Distribution: Madagascar.

Philosepedon flavithorax (Satchell) new combination

Trichopsychoda flavithorax Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 52.

Distribution: Malaya.

Philosepedon humeralis (Meigen)

Psychoda humeralis Meigen, 1818, Syst Beschr. 1(7): 106; Eaton, 1893, Ent. Mo. Mag. (2) 4: 33; Rapp and Cooper, 1945, Jour. N. Y. Ent. Soc. 53: 124; Freeman, 1950, Hndbk. Ident. Brit. Ins. 9(2): 91, 95.

Philosepedon humeralis, Eaton, 1904, Ent. Mo. Mag. (2) 15: 57; 1913, Trans. Linn. Soc. London, (2) 15: 429; Spärck, 1920, København Ent. Medd. 13: 120.

Psychoda (Philosepedon) humeralis, Tonnoir, 1919, Ann. Soc. Ent. Belg. 59: 14; 1922, ibid., 62: 61; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 87; Jung, 1956, Deutsche Ent. Zeitschr. (n.F.) 3: 190, 201.

Distribution: Europe, Great Britain, Seychelle Isl.

Philosepedon interdicta (Dyar), new combination

Psychoda interdicta Dyar, 1928, Proc. Ent. Soc. Wash. 30: 88; del Rosario, 1936, Philip. Jour. Sci. 59: 109; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 206; 1945, ibid. 53: 209; Quate, 1955, Univ. Calif. Publ. Ent. 10: 227.

Distribution: eastern U. S., West Indies.

Philosepedon maderensis (Satchell) new combination

Trichopsychoda maderensis Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 56.

Distribution: Madeira.

Philosepedon malayensis (Satchell) new combination

Trichopsychoda malayensis Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 55.

Distribution: Malaya.

Philosepedon mayeri (Satchell), new combination

Trichopsychoda mayeri Satchell, 1955, Proc. Roy. Ent. Soc. London (B) 24: 54.

Distribution: Austria.

Philosepedon opposita (Banks), new combination

Psychoda opposita Banks, 1901, Canad. Ent. 33: 274; Haseman, 1907, Trans. Amer. Ent. Soc. 33: 321; Johnson, 1925, Occ. Papers Boston Soc. Nat. Hist. 7(15): 45; del Rosario, 1936, Philip. Jour. Sci., 59: 121; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 86; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 207; Quate, 1955, Univ. Calif. Publ. Ent. 10: 230.

Distribution: eastern U. S. to Iowa and Texas.

Philosepedon tesca (Quate), new combination

Psychoda tesca Quate, 1955, Univ. Calif. Publ. Ent. 10: 229.

Distribution: California.

Philosepedon triangulata Eaton

Philosepedon triangulatus Eaton, 1913, Trans. Linn. Soc. London (2) 15: 429.

Psychoda (Philosepedon) triangulatus, Tonnoir, 1922, Ann. Soc. Ent. Belg. 62: 61; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 87.

Distribution: Seychelle Isl.

Philosepedon triastyla (Quate), new combination

Psychoda triastyla Quate, 1957, Nat. Malgache, 9: 259.

Distribution: Madagascar.

Philosepedon tridactila (Kincaid) new combination

Pericoma tridactila Kincaid, 1899, Ent. News, 10: 32.

Psychoda tridactila, Haseman, 1907, Trans. Amer. Ent. Soc. 33: 304; del Rosario, 1936, Philip. Jour. Sci. 59: 135; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 208; Quate, 1955, Univ. Calif. Publ. Ent. 10: 225.

Distribution: western United States.

Genus **Threticus** Eaton

Threticus Eaton, 1904, Ent. Mo. Mag. (2) 15: 57; Tonnoir, 1922, Ann. Soc. Ent. Belg. 62: 65 (subgenus); Enderlein, 1935, Sitz. Gesell. Natur. Freunde 1935: 249; 1936, Tier. Mitteleur. 6(16): 29; 1937, Deutsche Ent. Zeitschr. 1936: 86 (subgenus); Rapp, 1945, Bull. Brooklyn Ent. Soc. 40: 177; Jung, 1956, Deutsche Ent. Zeitschr. (n.F.) 3: 190 (subgenus) (gender masculine).

Adult.—Head: vertex long, two or three times as long as width of eye bridge; eye bridge with four rows of facets. Labellum bulbous (fig. 3), apically with bristles, but without teeth; palpus long, longer than entire length of head from posterior margin to apex of mouth parts, first palpal segment short, one-half or less length of third and fourth segments. Antenna with 16 segments, terminal 3 reduced and almost always separated; sensory filaments consisting of single branch, moderately sinuous.

Wing moderately broad; forks R_{2+3} usually distad of M_{1+2} by distance equal to more than three times width of cell R_2 at point of bifurcation; forks complete; R_5 ending at wing apex; membrane without vestiture.

Male genitalia: surstyle short and usually stocky, not much longer than 9th tergite, bearing one to four tenacula; aedeagus asymmetrical, unpaired lateral shaft much different from central shaft.

Female genitalia: genital digit absent. Subgenital plate bilobed, but apical concavity small.

Type species: *Psychoda lucifuga* Walker (by subsequent selection, Enderlein, 1935, Sitz. Gesell. Natur. Freunde, p. 249).

Distribution: Holarctic, Ethiopian, Australasian.

As with the preceding genus, the mouth parts of the species of *Threticus* differ fundamentally from those of *Psychoda* species. The structure

of the antennal sensory filaments is unique among the Psychoidini in being formed of a single unbranched element rather than the usual Y-shape.

INCLUDED SPECIES

Threticus aenigmaticus (Satchell) new combination

Psychoda aenigmatica Satchell, 1953, Austral. Jour. Zool., 1: 376.

Distribution: Tasmania.

Threticus bicolor (Banks), new combination

Psychoda bicolor Banks, 1894, Canad. Ent. 26: 33; 1901, ibid. 33: 275; Haseman, 1907, Trans. Amer. Ent. Soc. 33: 314; Banks, 1932, Bull. Brooklyn Ent. Soc. 26: 227; del Rosario, 1936, Philip. Jour. Sci. 59: 116; Enderlein, 1937, Deutsche Ent. Zeitschr. 1936: 86; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 205; Quate, 1955, Univ. Calif. Publ. Ent. 10: 233.

Distribution: eastern United States; Quebec, Ontario.

Threticus dubitatus (Tonnoir), new combination

Psychoda dubitata Tonnoir, 1939, Ruwenzori Exp., Brit. Mus. 1(4): 57.

Distribution: Kenya, Africa.

Threticus irroratus (Satchell), new combination

Psychoda irrorata Satchell, 1953, Austral. Jour. Zool. 1: 379.

Distribution: Tasmania.

Threticus jonesi (Quate), new combination

Psychoda jonesi Quate, 1955, Univ. Calif. Publ. Ent. 10: 231, 253.

Distribution: eastern United States.

Threticus lucifugus (Walker)

Pericoma lucifuga Walker, 1856, Ins. Brit. 3(1): 257.

Psychoda lucifuga, Eaton, 1893, Ent. Mo. Mag. (2) 4: 129; 1894, ibid. 5: 23; Rapp and Cooper, 1945, Jour. N. Y. Ent. Soc. 53: 124; Freeman, 1950, Hndbk. Ident. Brit. Ins. 9(2): 91, 95.

Threticus lucifugus, Eaton, 1904, Ent. Mo. Mag. (2) 15: 57.

Psychoda (*Threticus*) *lucifuga*, Tonnoir, 1919, Ann. Soc. Ent. Belg. 59: 14; 1922 ibid. 62: 65; 1940 Trans. Soc. Brit. Ent. 7: 32; Jung, 1956, Deutsche Ent. Zeitschr. (n.F.) 3: 190, 201.

Distribution: western Europe, Great Britain.

Threticus philpotti (Satchell), new combination

Psychoda philpotti Satchell, 1950, Trans. R. Ent. Soc. London, 101: 175; 1954, ibid., 105: 478.

Distribution: New Zealand.

Threticus unimaculatus (Satchell) new combination

Psychoda unimaculata Satchell, 1953, Austral. Jour. Zool. 1: 378.

Distribution: Tasmania.

In the opinion of Tonnoir (1922, Ann. Soc. Ent. Belg. 62: 65) the short, stocky surstyle of the male genitalia was the chief characteristic of *Threticus*, and on this basis he placed several species in it that properly belong to *Psychoda*. These species, *cinerea* Banks (=*compar* Eaton), *gemina* Eaton, and *obscura* Tonnoir, are not congeneric with the species of *Threticus*, as they possess the flattened labellum found only in the genus *Psychoda*.

Eurygarka,[2] new genus

Adult.—Head: vertex long, about one and one-half times as long as width of eye bridge; eye bridge with four rows of facets. Labellum bulbous, apically with bristles, but without teeth, palpus long, longer than length of head, first palpal segment short, less than one-half length of third and fourth segments. Antenna with 16 segments, terminal 3 reduced and clearly separated; sensory filaments consisting of a pair of broad, leaflike blades, each blade with 4 to 6 longitudinal veins.

Wing moderately broad; fork R_{2+3} distad of M_{1+2} by distance equal to little more than width of cell R_2 at point of bifurcation; forks complete; R_5 ending at wing apex; membrane without vestiture.

Male genitalia: surstyle short and stocky, shorter than ninth tergite, bearing two tenacula; aedeagus symmetrical, consisting of straight main shaft flanked by pair of rods.

Female genitalia: genital digit absent; subgenital plate not bilobed, tapering to rounded apex with no apical concavity; spermatheca smaller than in species of *Psychoda*, but of similar structure; cercus (ovipositor) subquadrate, not long and tapering.

Type species: *Psychoda helicis* Dyar, by present designation.

Distribution: Neotropical mainly.

The most conspicuous differences between this genus and others of the Psychodini are the leaflike structure of the antennal sensory filaments, the unilobate female subgenital plate and the short, broad, subquadrangular female cerci.

INCLUDED SPECIES

Eurygarka helicis (Dyar), new combination

Psychoda helicis Dyar, 1929, Proc. Ent. Soc. Wash. 31: 64; del Rosario, 1936, Philip. Jour. Sci. 59: 134; Rapp, 1944, Jour. N. Y. Ent. Soc. 52: 205; 1945, Jour. N. Y. Ent. Soc. 53: 29; Quate, 1955, Univ. Calif. Publ. Ent. 10: 235.

Distribution: southeastern United States, West Indies.

Genus **Psychoda** Latreille

Psychoda Latreille, 1796 Précis. caract. gén. ins. p. 152; 1802, Hist. Nat. Crust. Ins. 3: 424; Quate, 1955, Univ. Calif. Publ. Ent. 10: 191, 252 (bibliography); Jung, 1956, Deutsche Ent. Zeitschr. (n.F.) 3: 187, 192.

Tinearia Schellenberg, 1803, Gattungen der Fliegen, pl. 40. (Type species: *Psychoda alternata* Say, by subsequent selection, Coquillett, 1910.)

Trichoptera Meigen, 1803, Illiger's Mag. 2: 261. (Type species: *Tipula phalaenoides* Linnaeus, by subsequent selection, Coquillett, 1910.)

[2]Eurygarka—Gr., *eurys*–broad; *garka*–rod; referring to broad sensory filaments of antenna. Gender feminine.

Logima Eaton, 1904, Ent. Mo. Mag. (2) 15: 58; Tonnoir, 1922, Ann. Soc. Ent. Belg. 62: 63 (subgenus of *Psychoda*); Enderlein, 1935, Gesell. Natur. Freunde, 1935: 248; 1936, Tier. Mitteleur. 6(16): 29. (Type species: *Psychoda erminea* Eaton, by original designation and monotypic.)

Adult.—Head: vertex short, not extending above eyes more than distance equal to width of eye bridge; eye bridge usually with four rows of facets, rarely with three or five. Labellum (fig. 2) flattened and bearing about five teeth on apical margin; palpus equal to or shorter than length of head from posterior margin to apex of mouth parts, first palpal segment two-thirds or more length of following segments. Antenna with 14, 15, or 16 segments, terminal segments beyond 13 always reduced, about one-half size of preceding, often fused; sensory filaments Y-shaped, rarely with three anterior branches.

Wing: fork R_{2+3} distad of M_{1+2} by varying distances, forks generally complete, though bases of R_3 and M_2 lacking in many species; R_5 ending at wing apex; membrane without vestiture.

Male genitalia: surstyle most often slender and considerably longer than ninth tergite but may be short and stocky, bearing single tenaculum; aedeagus (fig. 5) asymmetrical, consisting of main shaft flanked by smaller lateral shaft on left side.

Female genitalia: genital digit almost always present. Cerci longer than subgenital plate; subgenital plate bilobed.

Type species: *Tipula phalaenoides* Linnaeus (by monotypy).

Distribution: cosmopolitan.

Tinearia is clearly a synonym of *Psychoda*, as its type species, *alternata*, is quite closely related to other members of the genus. Although the species is allied to a cluster of closely related, monophyletic species forming a minor division within the genus, there are no grounds for recognizing a separate subgroup. *Trichoptera* is identical with *Psychoda*, as these two genera are isogenotypic. *Logima* was erected on the basis of absence of erect hairs on veins R_3, R_5, M_2 and A (Cu_2, Tonnoir, 1922). However, this does not warrant another subgroup and is of even less significance than the standing of the *alternata* complex.

Genus **Termitadelphos** Holmgren

Termitadelphos Holmgren, 1905, Zool. Anz. 29: 530; Speiser, 1906, ibid., 30: 176; Edwards, *in* Tonnoir, 1929, Dipt. Patagonia and So. Chile, Brit. Mus. (Nat. Hist.), Pt. 2, 1: 2; Fairchild, 1951, Bull. Brooklyn Ent. Soc. 46: 15.

Type species: *Termitadelphos silvestrii* Holmgren (by monotypy).

From the illustrations provided by Holmgren, *Termitadelphos* appears to be synonymous with either *Threticus* or *Philosepedon*. It is not possible to be certain of its position without examination of specimens, in spite of Edwards' (1929) statement that it is clearly a synonym of *Psychoda*.

The genus was based on a single specimen collected in the nest of the termite *Eutermes rotundiceps* Holmgren and assumed to be a termitophilous fly. While this assumption may be correct, it is also possible that its presence in the nest was quite accidental, as psychodids are often found in dark, protected places.

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MICROFLORA ASSOCIATED WITH THE CONFUSED FLOUR BEETLE, TRIBOLIUM CONFUSUM[1]

J. H. VAN WYK, A. C. HODSON, AND C. M. CHRISTENSEN[2]

ABSTRACT

Larger numbers of bacteria and lesser numbers of storage fungi were isolated from larvae and adults of *Tribolium confusum* Duv., and the bacteria were more numerous in the insects than in the food from which the insects were taken. These bacteria, when added to autoclaved whole wheat flour, promoted growth and reproduction of *T. confusum*, but spores of the fungi had little beneficial effect on the insect. Addition of these bacteria to a vitamin-free diet allowed normal development of larvae. In free-choice and olfactometer tests, more adult beetles were attracted to autoclaved flour containing spores of storage fungi, and to autoclaved flour containing bacteria isolated from the insect, than to autoclaved flour alone. The continued presence or increase of *T. confusum* adults in flour or wheat was always accompanied by a decrease in storage fungi and an increase in bacteria. More adult beetles survived in moldy wheat than inm old-free wheat, at relative humidities of 60% and 75%. Volatile quinones secreted by the adult beetles were relatively toxic to the storage fungi and to some bacteria even when the beetles were not in contact with them. When *T. confusum* and *Sitophilus oryza* (L.) were reared together in wheat at a moisture content of 16%–17%, populations of bacteria and storage fungi increased greatly, but with fewer molds than when *S. oryza* was reared alone.

Tribolium confusum Duval has long been a favorite subject for the study of population dynamics, and many factors that influence the rise and fall of its populations have been worked out in some detail. So far as the writers are aware, however, the possible role of microflora in the economy of these insects has not been investigated. Agrawal et al. (1957) found that increasing populations of the granary weevil *Sitophilus granarius* (L.) in wheat were almost always accompanied by rapidly increasing numbers of storage fungi that contribute to rapid deterioration of the infested grain. Flour is known to harbor a moderate to heavy load of a considerable variety of fungi, yeasts, and bacteria (Christensen and Cohen 1950; Thatcher et al. 1953); it was thought possible that some of these microflora might influence or be influenced by developing populations of *T. confusum*, and the present work was undertaken to explore this.[3]

MATERIALS AND METHODS

The insect.—Cultures of *Tribolium confusum* were maintained on "Occident" brand whole wheat flour, which had a very low count of microflora, plus 5% by weight of dry brewers yeast. The flour and beetles used for egg production were changed periodically to keep them fresh, and eggs were sifted out weekly and placed in quart fruit jars half-filled with whole wheat flour. The cultures were kept in an incubator at 28° C.

Numbers and kinds of microflora in flour.—One gram of flour was placed in 99 ml. of sterile 0.2% agar solution, shaken briskly to suspend the material, successive dilutions were made by placing 5 ml. of this suspension in 45 ml. of the same agar solution, 1 ml. aliquots of one or more of the diluted suspensions were put in each of two or more petri dishes, melted agar cooled to 50° C. added, the dishes swirled to distribute the suspended material uniformly, the agar allowed to harden, and the dishes incubated until the colonies could be counted and identified. This is the procedure specified in Cereal Laboratory Methods, 6th ed. (1957). Usually, dilution cultures were made in malt-salt agar to detect storage fungi, in acid potato-dextrose agar to detect yeasts, and in bacto-peptone agar to detect bacteria.

Moisture content was determined by the two-stage, air oven method specified by Cereal Laboratory Methods (1957), and is expressed on a wet weight basis.

RESULTS

Microflora on and in different stages of the insect, and in flour.—Eggs, larvae, pupae, and adults of *T. confusum* were cultured without surface disinfection, and after washing for 1 to 2 minutes in 1% sodium hypochlorite followed by two rinses in sterile water. No microflora were obtained from surface-disinfected eggs, although the treatment did not kill the eggs. Non-surface-disinfected eggs yielded bacteria and some fungi, principally *Aspergillus glaucus*, *A. flavus*, *A. candidus*, and *Penicillium*, which presumably came from contaminating spores in the flour that adhered to the eggs. Both the non-surface-disinfected larvae and the surface-disinfected larvae yielded bacteria and the fungi listed above; usually fewer colonies grew from the surface-disinfected larvae than from those not surface-disinfected. When living larvae were cultured,

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they crawled over the surface of the agar, and left trails of bacteria and fungi, as shown in figure 1; this was true of those that had been surface-disinfected as well as those that had not been. Evidently the larvae ingest a variety of microflora from the flour on which they feed, and at least some of the microflora survive passage through the gut. The results with pupae were essentially the same as with the larvae: bacteria and fungi grew from both the non-surface-disinfected and the surface-disinfected pupae, but fewer colonies arose from those that were surface-disinfected than from those that were not. A typical example is shown in figure 2. When living adults were cultured without surface disinfection, hundreds of colonies of *Aspergillus glaucus*, *A. flavus*, and *A. candidus* grew up in their tracks on malt-salt agar; on bacto-peptone agar, bacteria grew in the tracks. Intestines dissected from surface-disinfected adults yielded bacteria, but no fungi or yeasts. Since fungi were obtained from some surface-disinfected adults, it was expected that the intestines would harbor these same fungi; however, only 10 intestines were cultured on malt-salt agar, and the evidence probably indicates only that fungi are not prevalent in the gut.

One-gram quantities of eggs, larvae and adults, not surface-disinfected and surface-disinfected, were comminuted in sterile 0.2% agar solution in a Waring blender, the suspension diluted and cultured, with the results given in table 1.

Table 1.—Number of colonies of bacteria and fungi isolated per gram of flour, and per gram of eggs, larvae, and adults of *T. confusum*

Material	Bacteria/gram (thousands)	Fungi/gram (thousands)
Flour	141	1.4
T. confusum		
Eggs	19.6	0.2
Larvae		
Not surface-disinfected	4,100	0.9
Surface-disinfected	1,200	0.2
Adults		
Not surface-disinfected	25,750	0.0
Surface-disinfected	15,100	0.0

The results of this aspect of the work indicated that while the common fungi in flour, principally *Aspergillus* and *Penicillium*, might survive in small numbers within and on the outside of larvae and adults of *Tribolium*, they evidently were not increasing, either in the flour inhabited by the

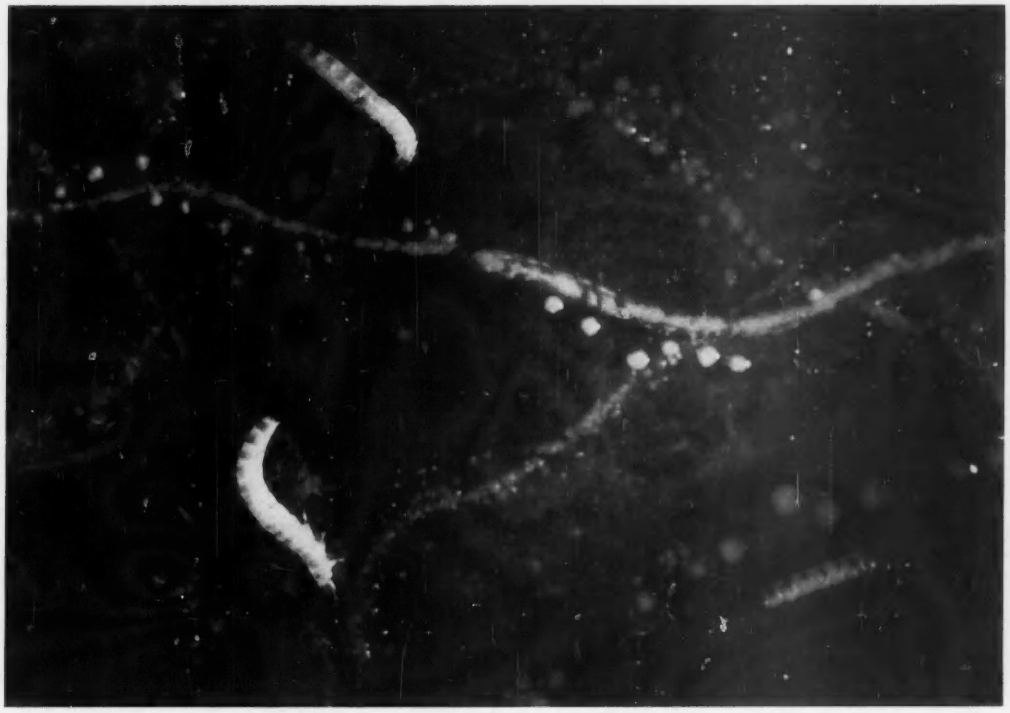

FIG. 1.—Larvae of *T. confusum*, not surface-disinfected, on the surface of an agar medium, their tracks marked by colonies of bacteria.

insect, or within the insect. There was no increase in the fungi, as was detected by Agrawal et al. (1957) in grain inhabited by *Sitophilus granarius* (L.). Both larvae and adults, however,

Table 2.—Duration of larval stage of *T. confusum* on nonautoclaved flour, and on autoclaved flour plus bacteria and fungi

Flour	Days to pupation[2]	
	Average	Range
Nonautoclaved	19	18–24
Autoclaved[1]	38	26–51
+bacteria	22	20–25
+fungi	35	26–41
+nutrient broth	36	26–45

[1]Sterile water added.
[2]All larvae pupated.

yielded many more colonies of bacteria than did an equal weight of flour; thus it seems probable that the bacteria are increasing within the insect. The possible role of these bacteria, as well as of some of the common fungi that occur in flour, in the economy of the insect was explored further.

Effect of microflora isolated from T. confusum upon growth and reproduction of the beetle.—Whole-wheat flour was autoclaved twice for 1 hour at 15 lbs. pressure, with an interval of 2 days between the first and second autoclaving. Bacteria isolated from *Tribolium* were inoculated into sterile 2% bacto-peptone nutrient broth, incubated for 1 week, and dilutions were cultured, at which time each ml. of broth contained 193,000,000 bacteria. One ml. of this suspension was added to each of three replicate 2-g. samples of flour. One ml. of sterile broth was added to each 2-g. control. The excess liquid was allowed to evaporate. An inoculating needle loopful of spores of *Aspergillus candidus*, *A. flavus*, and *A. repens* in 1 ml. of water were similarly added to 2-g. portions, duplicate samples being used for each fungus. One ml. of sterile water was added to each of the controls.

Eggs of *T. confusum* were placed on filter paper, washed for 1½ minutes in 2% sodium hypochlorite, rinsed in sterile water, and placed in a sterile desiccator containing a saturated solution of KCl to maintain a relative humidity of 85%, and the desiccator kept at 28° C. As the eggs hatched, the larvae were removed with a sterile brush and placed on the various foods. All were placed in sterile desiccators containing a saturated solution of NaCl to maintain a relative humidity of 75–76%, in equilibrium with a moisture content of 15% in the flour. All were kept at 28° C. The duration of the larval stage on each of the

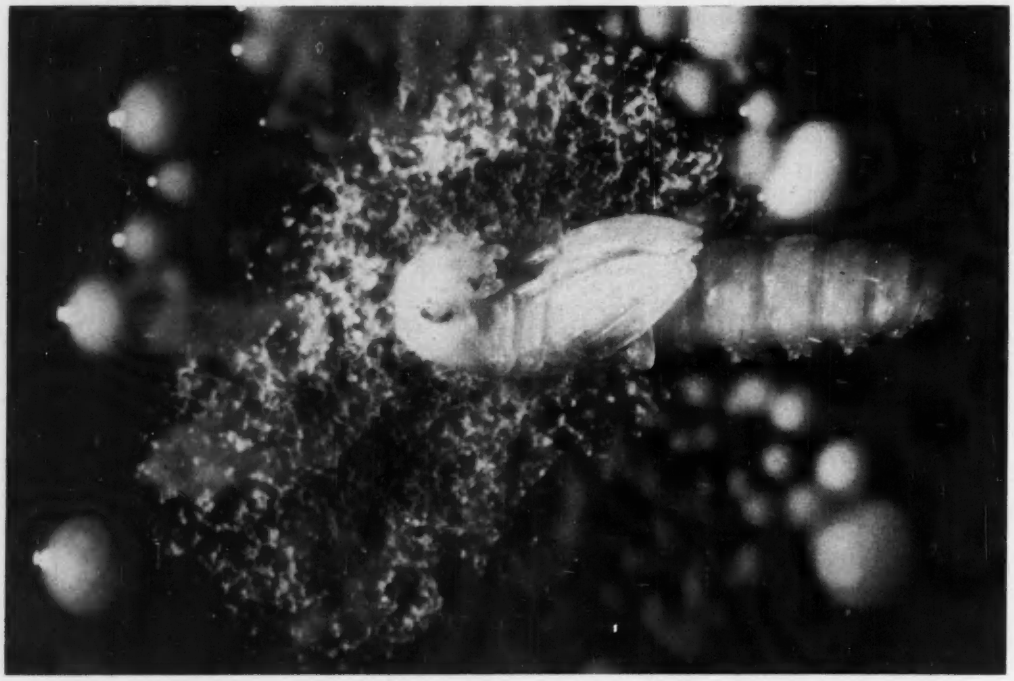

FIG. 2.—Surface-disinfected pupa of *T. confusum* cultured on bacto-peptone agar; bacteria and a fungus (probably *Aspergillus*) have grown from it.

Table 3.—Number of eggs produced by *T. confusum* reared on nonautoclaved flour, and on autoclaved flour plus bacteria and fungi.[1]

Substrate on which larvae were reared[2]	Number of eggs laid by 5 females each week				Total	Average number of eggs/female/week
Week	1	2	3	4		
Nonautoclaved flour	138	162	295	269	865	43
Autoclaved flour	81	115	143	128	467	23
+bacteria	191	192	327	314	1024	51
+fungi	93	131	154	138	516	26
+nutrient broth	82	133	157	140	512	26

[1]Five females and five males in each sample.
[2]Adults on whole-wheat flour during oviposition period.

foods was recorded, and is given in table 2. In the nonautoclaved flour and the autoclaved flour to which bacteria had been added, pupation was complete by the 25th day. In the other foods, pupation did not begin until the 26th day, proceeded very slowly, and was completed much later, although there was 100 percent pupation on all diets. This indicates that the bacteria isolated from *T. confusum* are able to supply the insect with some beneficial nutrient or nutrients.

Replicate samples, each sample consisting of five males and five females, were removed from each of the five substrates, placed in 20 g. of whole-wheat flour, and kept at 75% relative humidity and 28° C. The eggs deposited were sifted out every week for 4 weeks, and counted, with the results shown in table 3.

The adults from larvae reared on autoclaved whole-wheat flour plus bacteria produced approximately 15% more eggs than the adults from larvae reared on the nonautoclaved flour, and nearly 100% more than the adults from larvae reared on any of the other three substrates. This substantiates the evidence presented above, that the bacteria isolated from the beetle play a beneficial role in the economy of the insect.

Eggs were obtained from each of the five sets of adults, and kept under conditions optimum for hatching. No significant difference was observed in the percentages of eggs that hatched. Triplicate samples of larvae 1 day old, each sample consisting of 100 larvae, were taken from each of the 5 sets, placed in whole-wheat flour, kept at 75% relative humidity and 28° C., and the duration of the larval stage recorded. The results are given in table 4.

The differences here were of about the same magnitude as those in the first generation (table 2). Apparently the beneficial effect of the bacteria in the first generation persisted through the second generation even though, in the second generation, the egg-laying adults and larvae were fed whole-wheat flour.

Accessory growth factors produced by mircoflora associated with T. confusum.—A diet free of vitamins was compounded, consisting of 50 parts casein (casein E., ashless and vitamin-free, Glaxo Laboratories), 50 parts starch, 1 part cholesterol, 1 part McCollum's salt mixture No. 185, and 15 parts water. The casein, starch, and cholesterol were mixed together dry, the salt dissolved in water and this added to the other ingredients, and the whole mixed thoroughly. Two grams of this food was put in each petri dish, and three replicate dishes were used for each test.

Table 4.—Growth of second-generation larvae of *T. confusum* on whole-wheat flour after rearing first generation on nonautoclaved, and on autoclaved flour plus bacteria and fungi

1st generation reared on	Days to pupation of 2nd generation larvae[2]	
	Average	Range
Nonautoclaved flour	23	18–28
Autoclaved flour[1]	33	26–44
+bacteria	20	18–24
+fungi	32	25–41
+nutrient broth	34	25–43

[1]Sterile water added.
[2]100 percent pupation.

To this basic, vitamin-free diet the following were added:

1. Bacteria isolated from *T. confusum* were inoculated into sterile nutrient broth, incubated for 1 week, 1 ml. of this bacterial suspension added to each of three replicate dishes of the food described above.
2. One ml. of sterile nutrient broth.
3. One loopful of spores of *Aspergillus candidus*, *A. repens*, *A. flavus*, and *Pencillium*, plus 1 ml. of sterile water.
4. One ml. of sterile water.
5. One-half gram of dried, debittered brewer's yeast (Glaxo Laboratories).
6. A combination of 1 and 3 above (bacteria plus fungi).
7. A combination of 2 and 3 (nutrient broth plus fungi).

The various foods were incubated for a week, and the by then rather crusty material broken into granular form with a sterile spatula. Eggs of *T. confusum* were surface-disinfected, placed in sterile dishes, and allowed to hatch. Thirty lar-

vae, 1-day-old, were added to each of the test dishes, and the dishes incubated at 75% relative humidity and 28° C. The moisture content of the food did not change appreciably during the test. The duration of the larval stage, and the number of larvae that pupated, were recorded. The data are summarized in table 5.

Table 5.—Duration of larval stage of *T. confusum*, and number pupating on basic diet alone, and on basic diet plus microflora (30 larvae for each replicate)

Diet	Duration of larval stage in days		Average number of pupae
	Average	Range	
Basic[1]	all larvae died		0
Basic +bacteria	48	40–54	28
Basic +fungi	87	84–90	2
Basic +Yeast	29	26–32	30
Basic +bacteria and fungi	41	36–46	30
Basic +nutrient broth and fungi	76	72–80	12
Basic +nutrient broth	all larvae died		0

[1]Basic diet consisted of casein, starch, cholesterol, and salts.

Judged by these criteria, the basic diet plus yeast was best, followed by the basic diet plus bacteria and fungi, and basic diet plus bacteria. The basic diet plus fungi, and the basic diet plus fungi and nutrient broth, supported only very poor growth; larval mortality was high, and only a few larvae pupated. The basic diet plus nutrient broth, and basic diet alone, were very unfavorable—all of the larvae died by the 26th to 31st day. The larvae fed readily on the basic diet plus fungi, but did not increase in size. Figure 3 illustrates typical sizes of larvae reared on four of the diets.

Fraenkel and Blewett (1943) found that yeast can supply the larvae of *Tribolium* with growth factors of the vitamin B complex. Results of our tests substantiate their conclusions, and also indicate that bacteria obtained from the beetles, and a combination of bacteria and fungi, permit normal, or almost normal, development of the larvae of *T. confusum*. The basic diet plus fungi was not adequate.

Relative attractiveness to T. confusum of flour and of flour plus microflora.—Two types of tests were used. In one, the insects were free to choose between flour, and flour to which bacteria or various fungi had been added, while the second made use of an olfactometer.

For the free-choice test, a wood box was constructed, 2 feet square and 6 inches high, the walls lined with glass to prevent escape of the insects. Sixteen holes, each 2 inches in diameter, were bored in the wood floor, deep enough to hold metal containers with their rims flush with the floor. Whole-wheat flour was autoclaved, and divided into three portions. One, with nothing added, served as control. One was inoculated with bacteria obtained from *Tribolium*, and the other was inoculated with a mixture of spores of *Aspergillus candidus*, *A. flavus*, *A. repens*, and *Penicillium*.. The foods were dried to a moisture content of 10.1%–10.5%, broken into granular form with a sterile spatula, and put in the metal containers, and these were placed in the holes in the box. In any one test autoclaved flour and one of the other foods were used. The tests were repeated four times, each time with freshly prepared flour and a new set of beetles. One hundred adult beetles, 1-week-old, were placed in the box in each test, left for 12 hours, then sifted out of each food and counted. The results are given in table 6.

Table 6.—Number of beetles attracted to autoclaved flour, and to autoclaved flour containing bacteria or spores of storage fungi. (100 beetles in four replicated tests)

Flour treatments compared	Average number of beetles
Autoclaved flour	18
Autoclaved flour + bacteria	82
Autocalved flour	12
Autocalved flour + spores of storage fungi	88

The olfactometer used was similar to that developed by Willis and Roth (1950). Ten adult beetles, 1-week-old, were put in each of the two chambers, and tested for response to odor, at 29°–31° C., and in darkness except for the time (approximately 5 seconds) required for each count. The intensity of reaction is expressed as a ratio, following the method used by Gunn (1937) in his studies on humidity. The results are summarized in table 7.

The odor of flour plus fungi and of flour plus bacteria attracted more beetles than did the odor of autoclaved flour alone, and the odor of flour plus fungi attracted more beetles than the odor of flour plus bacteria, both when tested against the odor of autoclaved flour alone and when tested against the odor of flour plus bacteria. In both the free-choice and the olfactometer tests, the beetles definitely were attracted preferentially to flour plus fungi. Judging by our own sense of smell, the fungi had a considerably stronger odor than the bacteria.

Changes in microflora of wheat and flour stored at different moisture contents, infested and not infested with T. confusum.—Agrawal et al. (1957) found that when granary weevils once became established in grain whose moisture content originally was below 13.5%, the lower limit where fungi can grow, the moisture content of the grain

Table 7.—Olfactometer tests of the attractiveness of autoclaved flour, with and without certain microflora, to *Tribolium confusum* beetles (20 beetles per test, and 10 counts at 1-minute intervals)

Flour treatments compared	Accumulative counts	Reaction ratios	Preference
Autoclaved/autoclaved	101/99	1.00	none
Autoclaved+fungi/autoclaved	149/51	2.92	autoclaved+fungi
Autoclaved+fungi/autoclaved+fungi	104/96	1.08	none
Autoclaved+bacteria/autoclaved	143/77	1.85	autoclaved+bacteria
Autoclaved+bacteria/autoclaved+bacteria	102/98	1.04	none
Autoclaved+fungi/autoclaved+bacteria	109/91	1.18	autoclaved+fungi
Autoclaved+nutrient broth/autoclaved	101/99	1.00	none

increased and fungi developed rapidly. *T. confusum* is known to be able to develop in flour at moisture contents well below 13.5%. There is little reliable evidence as to the lower limit of moisture content that will permit *T. confusum* to develop in grain. As pointed out by Agrawal et al. (1957), in the work by Daniels (1956) dealing with development of flour beetles in grain at different moisture contents, the moisture determinations were considerably in error.

Approximately 750 grams of flour or wheat were placed in the requisite number of quart fruit jars. The flour had a moisture content of 9.2%, and the wheat a moisture content of 9.9%. Two hundred adult beetles were added to each jar; noninoculated jars served as controls. The jars were kept at relative humidities of 45%, 60%, and 75%, at 25° C. At intervals of 1 month, moisture contents and numbers of fungi and bacteria were determined. The results are summarized in table 8.

The beetles developed, reproduced, and appeared to thrive normally in flour with an initial moisture content of less than 10%. However,

FIG 3.—Larvae of *T. confusum*, all 25 days old. The pairs, from left to right, were reared on basic diet plus: 1. Yeast; 2. Bacteria and fungi; 3. Nutrient broth and fungi; 4. Fungi.

Table 8.—Number of colonies of fungi and bacteria per gram of flour and wheat infested with *T. confusum* and stored 1–3 months at 25° C. and 45%, 60%, and 75% relative humidity[1]

Relative humidity %	Treatment	Moisture content % (Initial m.c. 9.2%)	Fungi/gram (thousands)	Bacteria/gram (thousands)
		Flour—1 month		
45	Infested	10.8	1.1	18
	Not infested	9.4	3.3	2.7
60	Infested	11.6	2.0	37
	Not infested	10.2	3.7	3.7
75	Infested	14.8	1.1	58
	Not infested	13.7	4.2	3.5
		Flour—2 months		
45	Infested	11.6	1.5	41
	Not infested	10.2	2.9	2.8
60	Infested	12.6	1.4	91
	Not infested	11.4	3.4	3.5
75	Infested	15.7	0.8	130
	Not infested	14.2	3.9	3.8
		Flour—3 months		
45	Infested	12.1	1.0	100
	Not infested	10.5	2.7	2.5
60	Infested	13.6	0.8	520
	Not infested	11.6	3.3	3.9
75	Infested	17.0	0.6	1160
	Not infested	14.6	3.8	4.2
		Wheat—1 month		
45	Infested	10.1	0.7	30
	Not infested	10.2	2.5	85
60	Infested	11.4	0.8	27
	Not infested	11.8	2.2	72
75	Infested	14.5	0.4	36
	Not infested	13.9	4.4	91

[1]200 adult beetles in 750 g. flour or wheat.

Table 9.—Survival and feeding of *T. confusum* adults in moldy and nonmoldy wheat stored 3 months at relative humidities of 45%, 60%, and 75%[1]

Relative humidity %	Average moisture content %	Average number of dead beetles	Average number of kernel germs eaten	Average weight of frass mg.
		1 month		
		Wheat moldy		
45	10.6	50	17.6	13.6
60	12.5	0.3	83	54.1
75	15.5	0	146	103.6
		Wheat not moldy		
45	10.6	50	26.3	16.7
60	12.5	17.3	92	61.3
75	15.6	8.3	121	95.3
		2 months		
		Wheat moldy		
60	12.8	50	117	67.5
75	15.8	24	183	140.6
		Wheat not moldy		
60	12.3	50	93	62.4
75	15.7	48	154	124.2
		3 months		
		Wheat moldy		
75	15.9	48	202	152.8
		Wheat not moldy		
75	15.7	50	156	124.4

[1]50 beetles in each of three replicates.

in 3 months the flour kept at 45% relative humidity had a moisture content of 12% where the beetles were present, while the flour without beetles at this relative humidity had a moisture content of 10.5%. With increasing relative humidity of storage, the increase in moisture content of the flour containing beetles was greater than that of the controls. In those lots held at a 75% relative humidity this difference would be of great biological significance for storage molds.

The number of colonies of fungi per gram of flour decreased with increasing time and with increasing relative humidity. In those stored at 75% relative humidity, for example, the moisture content had increased to approximately 17% after 3 months, and normally a considerable increase in fungi would have been expected, yet these samples had the lowest count of fungi of all. Evidently the fungi originally present were being eliminated, and they were being prevented from growing or reproducing even at moisture contents that normally should favor rather rapid growth and reproduction. The counts of bacteria, however, increased with increasing time of storage and increasing relative humidity. The bacteria presumably were increasing within the insects, and being excreted, since none of the samples of flour or grain had a high enough moisture content, even at the end of the tests, to support growth of bacteria.

The test with wheat was discontinued after 1 month, because at that time all of the beetles in the grain kept at relative humidities of 45% and 60% were dead, while in the grain at 75% relative humidity a few beetles were alive but no larvae were present. A relative humidity of 75% appears to be too low to support development of the insects in whole grain, even with the rather heavy infestation used here. Counts of both fungi and bacteria were lower where the beetles were present than in the controls.

Influence of storage fungi upon establishment of T. confusum in wheat.—As is evident from the work of Daniels (1956), under certain circumstances *Tribolium* can develop in and consume wheat kernels. In the tests described above, in which the beetles did not survive for long in whole grain even at a relative humidity of 75%, the grain was high-grade, seed-quality, and almost free of storage fungi. The same grain was used for the present tests, but one portion was stored dry in the laboratory, the other stored at a relative humidity of 80% for several months. At this time, the grain stored dry yielded 123 colonies of fungi and 3,800 colonies of bacteria per gram, while the grain stored at 80% relative humidity for several months yielded 164,000 colonies of storage fungi and 300,000 colonies of bacteria per gram. This was not excessively moldy or musty grain, and it is not unusual to encounter parcels of wheat from commercial storage that yield as many colonies of the same storage fungi as were present on this sample (Christensen 1951, 1955), especially if the grain has undergone some deterioration.

Both samples were dried to a moisture content of 8.4%, and portions of 20 grams were placed at relative humidities of 45%, 60%, and 75% for a week, after which the moisture contents of the moldy wheat were 10.5%, 11.8%, and 14.9%, respectively, and the moisture contents of the nearly mold-free wheat were 10.4%, 11.8%, and 14.8%, respectively. Fifty adult *T. confusum* were added to each sample, and the samples again placed at relative humidities of 45%, 60%, and 75%. Triplicate samples were used for each test. Samples were removed at intervals of a month, and the number of dead adults, total weight of frass, and number of grain germs eaten were determined. The results are presented in table 9.

At the end of 1 month in the grain at 45% relative humidity, all of the beetles were dead; somewhat more germs had been eaten, and somewhat more frass produced, in the nonmoldy than in the moldy grain. At 60% relative humidity, fewer beetles died in the moldy than in the nonmoldy grain. At 75% relative humidity, more beetles survived, more germs were eaten, and more frass produced in the moldy than in the nonmoldy grain.

After 2 months at 60% relative humidity, all of the beetles in both samples were dead, but more germs had been eaten and more frass produced in the moldy than in the nonmoldy grain. At 75% relative humidity, more beetles survived, more germs were eaten, and more frass was produced in the moldy than in the nonmoldy grain.

Judging from these results, at relative humidities of 60% and 75% moldy grain not only attracts *T. confusum*, as shown by the tests reported earlier, but also favors survival of the insect. It seems plausible that in some circumstances *T. confusum* might invade moldy grain, become established there, contribute to an increase in moisture content of the grain where it is established and also of the adjacent sound grain, and then move into the sound grain.

Effect on microflora of quinones produced by adult T. confusum.—Adults of *T. confusum*, especially when crowded or under stress, secrete volatile quinones that are toxic to the insects themselves (Goughm 1939, Shepard 1943), and De Coursey et al. (1953) found aqueous extracts of both common species of *Tribolium* to be toxic to many kinds of bacteria in vitro. It seemed likely that toxic action of these same compounds might explain the decrease in fungi in flour or grain where the beetles were present, as recorded in several of the present tests.

Spores of *Aspergillus candidus*, *A. flavus*, *A. repens*, *A. ruber*, and *Penicillium* were added to flour and wheat which already had a rather high count of bacteria. The flour or wheat was mixed

Table 10.—Microflora per gram of flour and wheat inoculated with spores of storage fungi, after which adult *T. confusum* or quinones were added, and the materials stored 3 weeks at 28° C. and 75% relative humidity

Treatment: Insects or quinones added	Moisture content %	Fungi/gram (thousands)	Bacteria/gram (thousands)
	Flour—1 week		
25 beetles	14.7	1210	132
50 beetles	14.9	895	22
100 beetles	15.5	660	6.8
2.8 mg. quinones	14.1	3.8	0
Control	14.1	1520	870
	Flour—2 weeks		
25 beetles	14.9	200	50
50 beetles	15.6	130	10
100 beetles	16.1	4.4	1200
2.8 mg. quinones	14.2	2.4	0
Control	14.4	1440	700
	Flour—3 weeks		
25 beetles	15.3	82	13
50 beetles	15.9	9.3	155
100 beetles	16.6	1.8	2020
2.8 mg. quinones	14.4	0.1	0
Control	14.5	1300	520
	Wheat—1 week		
25 beetles	14.9	18,700	520
50 beetles	15.1	13,500	116
100 beetles	15.7	490	9.2
2.8 mg. quinones	14.4	13.3	0
Control	14.3	22,000	2260
	Wheat—2 weeks		
25 beetles	15.1	890	135
50 beetles	15.5	510	16
100 beetles	15.8	118	78
2.8 mg. quinones	14.6	5.5	0
Control	14.5	10,100	1980
	Wheat—3 weeks		
25 beetles	15.5	320	6.2
50 beetles	15.8	145	42
100 beetles	16.4	9.1	1410
2.8 mg. quinones	14.6	0.3	0
Control	14.5	9,150	1795

thoroughly, and to triplicate samples of 50 grams each were added 25, 50, and 100 adult *T. confusum* 1-week-old, and 2.8 mg. of quinones from *T. confusum*,[4] approximately equal to the amount produced by 100 beetles. Nothing was added to the controls. The samples were kept at 75% relative humidity and 28° C., and were assayed for microflora at intervals of a week. The results are given in table 10.

The quinones added as such reduced the count of bacteria to zero within the first week, and greatly reduced the number of fungus colonies, especially in the first week. The number of fungus colonies decreased with time and with increasing number of beetles, but remained constant in the controls (the fungi would not be expected to increase in 3 weeks at the moisture contents used). Where the beetles were present, the count of bacteria at first decreased, but, where 50 and 100 beetles were present, the count of bacteria had increased sharply at the end of 3 weeks. Presumably these were bacteria multiplying within and being excreted by the insects.

In the flour and wheat without beetles, and in the flour and wheat infested with 25 beetles, the number of bacteria decreased with time. This decrease presumably was in bacteria naturally present in the wheat or flour. Such a decrease would be expected in grain or flour kept at 14% moisture content. Evidently a population of 25 beetles per 50 grams of flour or grain was too low to contribute, in 3 weeks, to a significant increase in the number of bacteria associated with the insect.

Fifty-gram quantities of wheat and flour contaminated with spores of storage fungi and bacteria were suspended in screw-cap bottles. One hundred, two hundred fifty, and five hundred beetles were placed in the bottom of each of two replicates, and 13.8 mg. quinones (approximately equal to the amount extracted from 500 beetles) in the bottom of another two replicates. Microfloral counts were made after 1 week, and are given in table 11.

[4]Obtained through the courtesy of L. M. Roth, Biology Branch, Hq. Quartermaster Research and Development Command, Natick, Massachusetts.

Evidently the volatile secretions of the insects are rather highly toxic to the common storage fungi and to the bacteria used in this test.

Table 11.—Microflora surviving in flour and wheat stored in a closed vessel above adults of *T. confusum* and above quinones, after 1 week at 14.5–14.8% moisture content

Stored above	Molds/gram (thousands)		Bacteria/gram (thousands)	
	Flour	Wheat	Flour	Wheat
100 beetles..	136	1370	375	990
250 beetles..	5.8	104	10.5	5
500 beetles..	0.3	———	0	———
13.8 mg. quinones..	0	0	0	0
Control.....	1620	35,000	10,600	39,000

It was thought possible that the volatile toxic compounds may have been absorbed on the flour or wheat and that this, when cultured, might have been toxic to the fungi or bacteria in the agar medium, although it may not have actually killed the organisms on the flour or wheat. To explore this, spores of several storage fungi and bacteria isolated from flour, wheat, and larvae and adults of *T. confusum* were added to 500 ml. of sterile 0.2% agar solution, shaken for 2 minutes, and divided into 100 ml. aliquots. To replicate suspensions were added: 1 gram of living *T. confusum* adults, 1-week-old, blenderized for 1½ minutes; 1 gram of *T. confusum* adults, 1-week-old, held in a vacuum oven (18 inches of Hg.) at 40° C. for 24 hours in an attempt to rid them of volatile materials; and 13.8 mg. quinone extract. Nothing was added to the controls. After 8 and 24 hours the suspensions were assayed for microflora and the results are given in table 12.

Both the quinones as such and the non-vacuum-treated, comminuted insects reduced the count of bacteria and fungi, especially after 24 hours. The material to which the vacuum-treated insects were added had a higher count than the controls of both bacteria and fungi; the most reasonable explanation of this, as far as we can now see, is that these beetles were contaminated with considerable numbers of both storage fungi and bacteria, and that the elimination of the toxic quinones by vacuum treatment allowed these organisms to grow.

Table 12.—Number of colonies of fungi and bacteria cultured from 100 ml. of 0.2% agar solution to which had been added comminuted adult *T. confusum* or quinones

Added to agar suspension	Fungi/gram (thousands)		Bacteria/gram (thousands)	
	8 hrs.	24 hrs.	8 hrs.	24 hrs.
1 g. comminuted live beetles.....	705	5.3	83	74
1 g. vacuum-treated and comminuted beetles.....	15,200	15,000	49,500	48,000
13.8 mg. quinones...	435	0.3	0	0
Control.....	8250	7950	23,000	23,000

Influence of a mixed population of T. confusum and Sitophilus oryza upon numbers and kinds of microflora in wheat.—Infestations of *Sitophilus* sometimes are accompanied or followed by infestions of *Tribolium*. It seemed interesting to determine the effect of each of these alone, and the two together, upon the microflora in grain. Wheat conditioned to a moisture content of 16% was divided into 50-gram portions, and replicate samples inoculated with *T. confusum* alone, *S. oryza* alone, and a combination of the two. Fifty adult beetles, 1-week-old, were placed in each bottle inoculated with each single species alone, and 50 of each in each bottle where the two were combined. Similar samples free of

Table 13.—Microfloral count of wheat infested with *T. confusum* and *S. oryza* alone and together and stored 3 months at 80% relative humidity

Grain infested with	Moisture content % (Initial m. c. 16.0%)	Fungi/gram (thousands)	Bacteria/gram (thousands)
	Stored 1 month		
T. confusum alone.....	16.7	4	3
S. oryza alone.....	17.1	47	420
T. confusum+*S. oryza*.....	17.2	32	290
Control.....	16.2	25	3
	Stored 2 months		
T. confusum alone.....	17.0	1.8	5
S. oryza alone.....	18.1	2035	5100
T. confusum+*S. oryza*.....	18.3	755	8100
Control.....	16.4	38	3
	Stored 3 months		
T. confusum alone.....	17.3	4	7
S. oryza alone.....	18.8	61,000	3,500,000
T. confusum+*S. oryza*.....	19.6	4,300	3,000,000
Control.....	16.6	55	3

insects were kept as controls. The grain was assayed for microflora at intervals of a month, with the results given in table 13.

In the culture of *S. oryza* alone, the storage fungi increased rather rapidly, as found by Agrawal et al. (1957) for *S. granarius*, but the number of bacteria also increased greatly (Agrawal et al. did not test their samples for bacteria). With *Tribolium* alone, the storage fungi decreased in number, as found in all other tests in this study, and the decrease was progressive with time. The population of bacteria increased somewhat, but by no means as much as in some of the previous tests. The ecological conditions, as indicated by wheat moisture content, were significantly different in the tests reported in tables 10 and 13. Whether these differences can account for the manyfold increase of bacteria in one case and not in the other is not known. Where both insects were present, both fungi and bacteria increased moderately in 1 month, and extensively in 2 and 3 months. Evidently the tendency of *S. oryza* to promote the development of fungi only partially offset the inhibiting influence of *T. confusum*. The moisture content of the grain also was increased as much as 3%.

There is considerable evidence in the literature that, in grain free of insects, bacteria do not increase measurably until the moisture content of the grain exceeds 18% (Milner et al. 1947), and in grain stored at moisture contents of 14%–18%, where storage fungi increase rapidly, the bacteria usually decrease in numbers. In the present tests, there was no increase in numbers of bacteria in the controls during the 3-month storage period. The great increase in numbers of bacteria in the samples where insects were present must be attributed to the activities of the insects, and it seems likely that the major source or reservoir of bacteria was the digestive tract of the beetles.

DISCUSSION

The pattern of association between microflora and insect appears to be considerably different in *Tribolium confusum* than has been found so far with *Sitophilus granarius*. The adult *T. confusum* are attracted to flour or grain contaminated with storage fungi such as *Aspergillus candidus*, *A. flavus*, *A. repens*, and *Penicillium*. The larvae and adults, whether in flour or in grain, consume some of the fungi, but only an occasional culture of storage fungi was isolated from the live beetles, even when they were feeding on obviously moldy material. The fungi evidently can contribute at least some of the B vitamins necessary for normal growth and reproduction of the insect, but do not appear to be a particularly good source of these vitamins. As the beetles develop in either flour or grain, the population of storage fungi decreases, sometimes almost to the vanishing point, presumably because of quinones, secreted by the beetles, which are toxic to the fungi. The insect may be attracted to and develop somewhat better in flour or wheat containing these storage fungi than in flour or wheat free of storage fungi, but, once established, tends to eliminate the fungi.

Certain bacteria, or a single kind of bacterium, grow in the gut of the insect. While flour contaminated with these bacteria was not appreciably more attractive to the insects than flour contaminated with spores of storage fungi, or was even less attractive, it furnished a better medium for growth and reproduction. The bacteria appeared to supply the B vitamins necessary to normal development of the insect about as effectively as did brewer's yeast; in a natural state these bacteria may contribute very significantly to the economy of the insect.

The rate of development of second-generation larvae was affected by the diets given the larvae of their parents. A poor diet in the parent-larval stage caused slow growth in the second generation, even when the adults of the second generation and their larval progeny were fed a whole-wheat flour diet. This phenomenon is similar to results obtained by Reynolds (1945), who found that the growth rate of second-generation larvae of *Tribolium destructor* was influenced by the quality of flour given to the parent generation.

Adult *T. confusum* were attracted to flour containing either storage fungi or bacteria isolated from the beetles themselves, and so the insects presumably possess some olfactory sense. The function of the malodorous secretions from the adult flour beetles has been a subject of much speculation; these compounds may have several different biological functions, of course, but one important function appears to be the suppression of storage fungi in the substrate, thus keeping the food material relatively free of a group of microflora that might, if allowed to grow unchecked, compete very directly with the insect, or make the substrate unsuitable for the insect.

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OBSERVATIONS ON THE LIFE HISTORY AND MORPHOLOGY OF KERMES PUBESCENS BOGUE (HOMOPTERA: COCCOIDEA: DACTYLOPIIDAE)[1]

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ABSTRACT

In Maryland there is one generation per year, on *Quercus alba*. Eggs are laid on new growth in late June and July. Crawlers migrate to the larger limbs and trunk of the host, where they insert their beaks and overwinter without apparent morphological change, the first molt occurring in May of the next year. Females then migrate to new growth, where the second and third molts occur, and reach maturity in late May and June. Males mature at the overwintering site. Although only 2.5 mm. in length, a single adult female feeding on a young leaf petiole or midvein can cause serious distortion. Some infestations were noted where "flagging" of 25 to 40 percent of the terminals of large trees had occurred after mid-July. The four female instars are described, as also the adult male. The number of instars in the life cycle of males was not determined.

The genus *Kermes* comprises a small group of oak-tree-infesting coccids. Fernald (1903) listed 28 species principally from the United States, Europe, and Japan. At present the list of *Kermes* from oak for the world contains 57 names. No *Kermes* are known to occur in Australia. Despite their wide distribution and rather common occurrence in certain areas, no member of this genus has been thoroughly studied from the morphological or biological standpoint in the United States. Two factors contributing to this situation are: (1) there is apparently only a single annual generation, and (2) the adult females develop very rapidly after the last molt, thereby allowing only a short space of time wherein good study material can be obtained. After this they become heavily sclerotized and greatly distended.

Ferris' (1920) first published illustration in this group was of *K. cockerelli* (Ehrhorn). Ferris (1955) recently illustrated the adults of three species of *Kermes*, two of these new, from the Southwestern United States. So far as the authors know, Ferris' illustrations are the first to show morphological details of adult females from the United States. Kuwana (1931) has published excellent illustrations of the larvae of three Japanese species. The work of Balachowsky (1950, 1953) presents a modern treatment of the European and Mediterranean species.

LIFE HISTORY

The adult females develop on the current seasons' growth of twigs, and on the petioles and principal veins of the leaves. In Maryland they began to lay eggs the latter part of June and continue to do so for about a month. The eggs hatch during the first week of July. The crawlers migrate immediately to the trunk and larger limbs of the host tree. They hide themselves in cracks and beneath loose bark and insert their beaks into the host's tissue, presumably to feed. While they are thus attached no appreciable growth changes occur until the following spring. Enormous numbers of viable crawlers can be found on some infested trees, but these populations gradually decrease during late summer and fall, apparently due to the activities of predators. The color of the first instar, or crawler, gradually changes from lemon yellow at hatching to a deep orange as winter approaches.

Growth activities of the host and insects begin about the same time in the spring. Course

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[2]Deceased May 11, 1958.

[3]The junior author revised slightly the manuscript prepared by the senior author and added the description of the male; he also made certain changes on drawings and prepared the drawing of the male.

strands of wax are secreted which eventually engulf the insects. At about the time the leaf buds unfold, the first stage insects are ready to molt. It has not been possible to differentiate between the sexes of the first instar, but the sexes can be separated after the first molt.

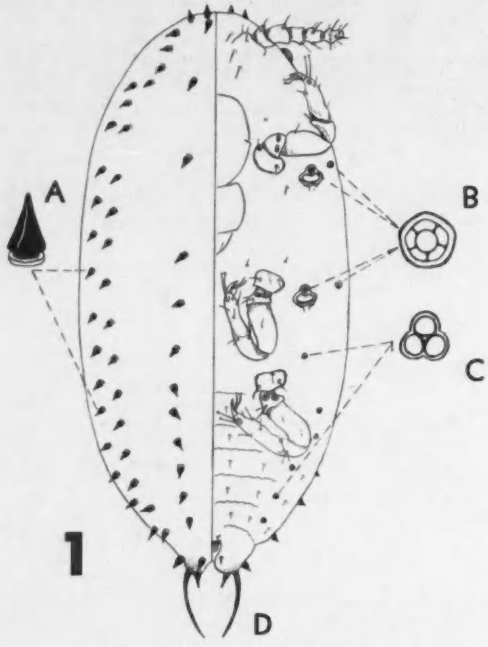

FIG. 1.—First instar or crawler.

Once the first molt is completed the females move from their hiding places on the trunk and limbs to the new growth. The second molt occurs about the second week in May, and the third molt the succeeding week. After the third molt the females grow very rapidly, and by the first week of June have become globular and and heavily sclerotized on the dorsal surface. Beginning with the second and third instars the females are engulfed in strands of coarse waxy filaments which are secreted principally by large tubular ducts along the margins and to some extent on the dorsal surface. Once the adult females have become well distended the discal portion of the dorsum is smooth and shiny, without any accumulation of a waxy pubescence.

Although only about 2.5 millimeters in length, a few females feeding on a young leaf petiole or midvein can cause serious distortion (figs. 6 and 7). Should several specimens feed in one area, the death of the leaf or twig may result. Some infestations were noted where "flagging" of 25 to 40 percent of the terminals of large trees had occurred after the middle of July. Thus infested shade and ornamental trees may have an unsightly appearance the latter part of the summer.

The development of the males takes a very different course. They do not migrate to the new growth after molting, but settle down in the same general area in which they overwintered. The males apparently do not feed after the first molt. Upon taking up their new position on the host, the males begin to secrete white, waxy, felted coccoons in which they will ultimately transform into winged adults.

MORPHOLOGY

First instar (fig. 1).—The crawlers vary in size from 0.7 mm. to 0.9 mm. long and 0.3 mm. to 0.5 mm. wide; are tapered at each end; have the dorsal margins beset with a more or less regular row of 16 pairs (on the average) of short, arrowhead-shaped setae (fig. 1A); have a single row of similar setae on each of the dorsal submedian areas, with apparently one seta on each abdominal and thoracic segment although segmentation of

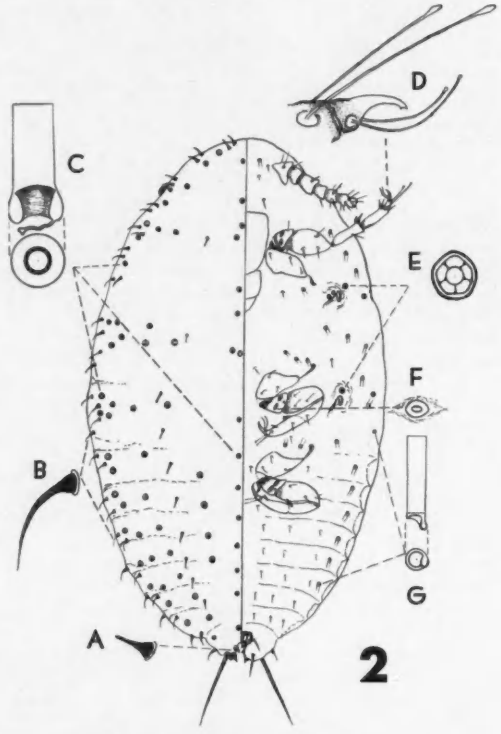

FIG. 2.—Second instar female.

these areas is not evident dorsally, and can be seen only faintly in the abdominal region on the ventral surface; have the anal lobes strongly developed, lightly sclerotized, bearing two setae along the mesal margin somewhat dorsally,

similar in shape to the marginal setae but usually longer, and each lobe with a typical stout, stiff, anal lobe seta (fig. 1D) about 250 microns long; have a porous anal ring with six short, stout, anal ring setae; have the ventral surface bearing a single row of 6 to 10 trilocular pores (fig. 1C) on each submargin, which are segmentally arranged; have six-segmented antennae beset with setae, the apical segment rounded and bearing the most setae; have rather stout, five-segmented legs, the tarsus longer than the tibia, with four sensory pits on each trochanter, two dorsal and two ventral in respect to the mounted specimen, and tarsus and claw each with a pair of slender, knobbed digitules longer than the claw; have two pairs of spiracles, the orifice being sclerotized, and at least one quinquelocular disc pore (fig. 1B) located on the anterior margin of the spiracles; and have a single quinquelocular pore located lateral to each spiracle on the margin.

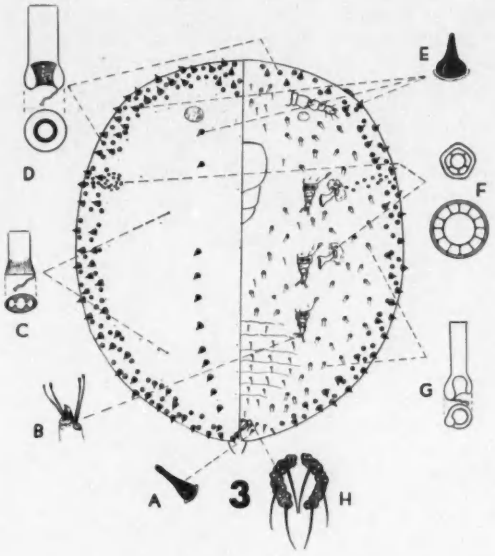

FIG. 3.—Third instar female.

Second Instar (fig. 2).—When attached to the host this stage is enveloped in coarse strands of wax which produce a pubescent effect. Mounted specimens are somewhat larger than first stage larvae, from 0.8 mm. to 1.1 mm. long and 0.3 mm. to 0.4 mm. wide, the ends rounded; with a slight constriction opposite each spiracle often noticeable; margins beset with a row of 18 pairs (on the average) of slender setae with flared bases (fig. 2B); with a single, dorsal, submedian row of similar setae on each side of the meson; ventral surface with a few, small, segmentally arranged setae on the abdomen and a few widely scattered over the rest of the venter; with strongly developed anal lobes, each bearing a pair of stout, elongate, blunt, tubercle-like setae (fig. 2A) on the mesal margin; with one typical, elongate, stiff, anal-lobe seta present on the apex of each anal lobe; with a strongly sclerotized anal ring with pores and six short, stout, anal ring setae; with six-segmented antennae located near the anterior margin; with five-segmented legs, the tibia and tarsus being nearly equal in length, each bearing a pair of short, stout setae antero-ventrally; with a pair of long, slender, knobbed digitules on the claw and tarsus (fig. 2D); with four sensory pits on the trochanter (fig. 2F), two ventral and two dorsal; with a large and strongly sclerotized mouth framework and two-segmented rostrum; with a pair of small spiracles, their orifices well sclerotized, the anterior pair with at least one quinquelocular pore (fig. 2E) located on the margin of atrium, and both anterior and posterior pairs flanked laterally by at least one similar pore; with two types of tubular ducts, one large, dorsally located, the cup atypical for the genus in that the sides are flared, producing a vasiform effect (fig. 2C), these ducts most prevalent along the margins and apparently arranged in segmental rows; ventral ducts smaller in diameter, and one side of the inner extremity enlarged, giving this type duct a signet-ring appearance (fig. 2G) in the second instar, and usually occur singly on the lateral aspects of the anterior abdominal segments, and rather generally on the ventral thoracic and head regions.

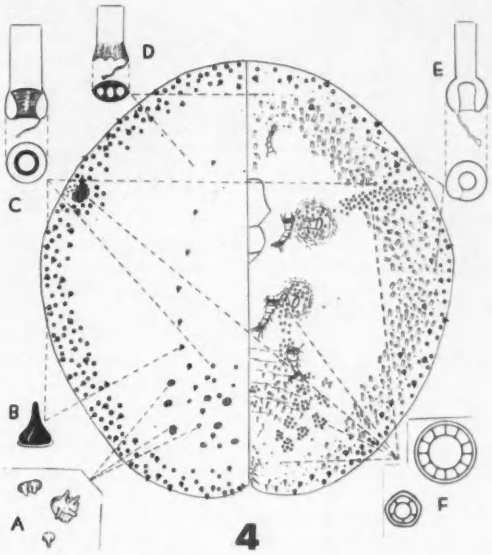

FIG. 4.—Adult female.

Third-Instar Female (fig. 3).—Mounted on

slides this stage varies from nearly round to slightly oval, length varying from 0.95 mm. to 1.65 mm. and width from 0.73 mm. to 1.3 mm.; with six-segmented antennae; with five-segmented legs, trochanter bearing two dorsal and two ventral sensory pits, the segments very short and

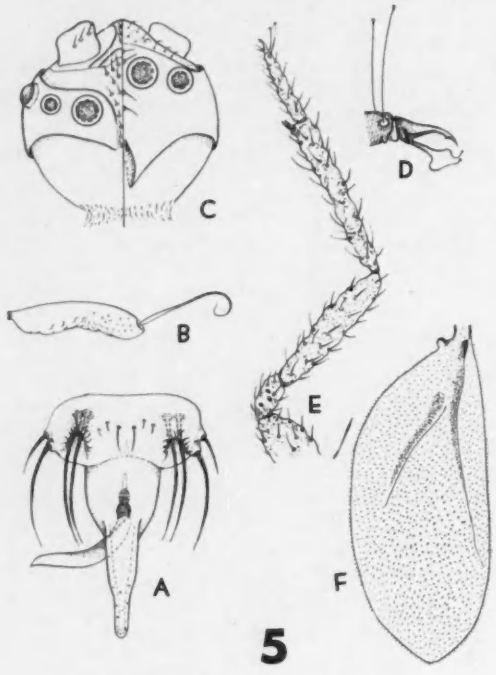

Fig. 5.—Adult male body parts.

stout, claw short and blunt, tarsal digitules long and slender, claw digitules about twice the length of the claw (fig. 3B); with anal lobes much reduced, mesal margins each with a pair of stout, top-shaped setae; with a heavily sclerotized anal ring (fig. 3H) bearing pores and six slender, elongate setae; with four types of setae present, the typical top-shaped marginal setae (fig. 3E) which may occur on both the dorsal and ventral margins depending on the position of the mounted specimen; 11 similar setae also occur in two submedian dorsal rows apparently segmentally arranged, a few small top-shaped setae may occur on the dorsal and ventral surface, several slender tubercular setae (fig. 3A) occur around the base of the reduced anal lobes on the ventral surface; with a pair of typical anal lobe setae present; and small, typical setae are present on the venter in segmental rows on the abdomen and scattered over the head and thoracic region; with four types of ducts and pores present; large cylindrical ducts with a vasiform cup (fig. 3D) on the dorsal and ventral margins intermingled with the top-shaped setae; more numerous but smaller, short ducts with extended, sclerotized, inner extremities, which are oval in surface view and appear to be bilocular or trilocular (fig. 3C), scattered over the dorsum and along the margins of the venter; many signet-ring-appearing ducts (fig. 3G) present over the entire venter, except in the region of the segmentally arranged setae; and lastly multilocular disc pores (fig. 3F) on the ventral surface in two areas—a band of pores extending from the anterior spiracle laterally to the margin and continuing for a short distance on the dorsal margin, terminating in a cluster of pores, and one to four pores present adjacent to the posterior spiracle; the number of loculi of these pores varying from 3 to 10; eyespots, if present, located lateral to the antennae; small sclerotized plates sometimes found on the derm, and if present usually occurring in pairs opposite each other, one ventral and one dorsal.

Unmounted Adult Female.—The full grown unmounted female appears small when compared with other species. It is globular in shape with the ventral surface flattened where it is attached to the host. It varies in size from 2.55 mm. to 3 mm. in diameter and 2 mm. to 2.5 mm. in height. The color varies considerably among individuals of the same or different stages; after becoming fully distended they take on shades of brown, from light to dark, but always with transverse bands of lighter brown. A rather striking feature of the fully distended female is a short stripe of snow white wax, 1 mm. or less in length, opposite each anterior spiracle, extending upward from the point of contact with the host. On unrubbed specimens, a short pencil of wax is seen at the apex of this stripe, the latter being formed by a tight group of multilocular disc pores on the anterior margin of the dorsum, which is the dorsal termination of the ventral transverse band of multilocular disc pores originating at the anterior spiracles. There are four evaginated sacs evident on the ventral surface, one rather round on each side of the mouth framework, and one elongate on each side of the posterior abdominal area. When females have developed to this point they are no longer suitable for mounting. The detailed microscopic features discussed below are from preparations of specimens that have recently molted the last time and are still more or less flat. At this stage they are lemon yellow in color.

Mounted Adult Female (fig. 4).—Antennae reduced, six-segmented, the three distal segments with the most setae; with reduced legs, similar to the preceeding stage in structure; with a large, heavily sclerotized mouth framework, and two-segmented rostrum; with large prominent spiracles, the anterior pair having a wide band of multilocular disc pores extending outward to, and slightly above the margin on to the dorsal surface; with the anal ring lacking pores, heavily scler-

otized; anal lobes not developed, anal lobe setae not present; top-shaped setae (fig. 4B) arranged in a widely scattered marginal band, some appearing on the dorsal and ventral surfaces as mounted, the outer setae of these bands may be more acutely pointed; a submedian row of similar

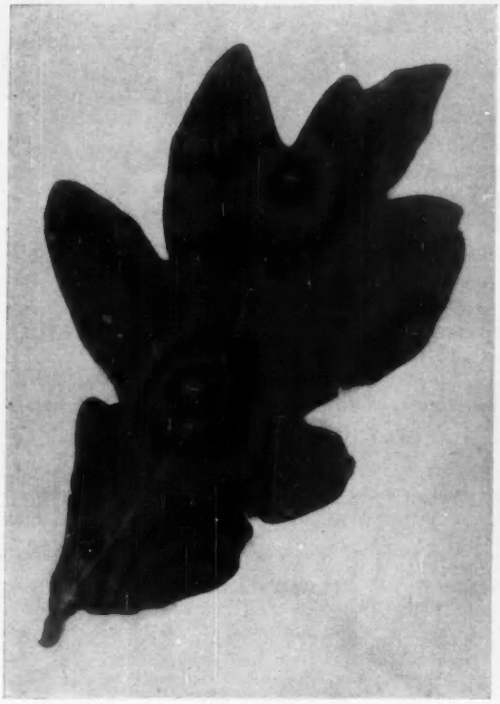

FIG. 6.—Adult females on the midvein causing leaf distortion.

setae present on both submedian dorsal areas, 10–11 in number; median ventral setae of the conventional type, small and slender, most of these in transverse segmental rows on the abdomen, and few widely scattered on other parts of the venter; two forms of tubular ducts on the dorsal surface, similar to those of the previous two instars, and two types on the ventral surface, differing somewhat in details from those of the two previous instars; dorsal ducts having a vasiform cup (fig. 4C) principally confined to the marginal area, mingled with the marginal band of top-shaped setae, but much more numerous and more widely scattered than the marginal setae, a few on the ventral submarginal area of the head, a group of 10 to 20 of these bordering each side of the band of multilocular disc pores that extends from the anterior spiracles to the margin; other dorsal ducts tiny, short, with internal end expanded, and sclerotized, and with a short delicate filamentous inner prolongation; in surface view these ducts, oval in shape, appearing to be bilocular or trilocular (fig. 4D) and evenly distributed over the dorsal surface; a conspicuous band of ventral ducts in the area extending around the body, except the posterior abdominal area, these ducts of the conventional form for the group, longer but smaller in diameter than the dorsal ducts with vasiform cups, the inner extremity of the tube enlarged, globular in outline, one-third to one-half wider than remainder of tube, cup cylindrical, with a filamentous inner prolongation, in the adult these ducts are not as conspicuously signet-ring-like as in previous instars, but are occasionally somewhat expanded at their inner extremity so as to appear iregularly bulged; ducts of the small dorsal type mingled with long ducts but absent on the remainder of the ventral surface; dorsal surface with a few papillae confined to the median and submedian posterior

FIG. 7.—Adult females distorting the petioles. (Photographs by Dr. Floyd Harrison, Department of Entomology, University of Maryland).

area of the abdomen (fig. 4A), these papillae occurring singly or in groups from two to five on definitely demarked raised areas of the derm, the individual papillae two to three microns in diameter, and three to four microns high, more

or less gradually tapered from the base to a pointed apex; ventral surface with mutlilocular disc pores associated with spiracles and in segmentally arranged groups on the posterior abdomen, the anterior spiracles with 20 to 30 grouped around the atrium; a crowded, more or less circular group at or above the margin opposite the anterior spiracle, a band four to seven pores wide extending inward from the above group toward the spiracle, but usually not reaching it; posterior spiracle with 15 to 20 pores around the atrium, and an occasional pore between the spiracle and the margin; abdominal segments with two more or less circular groups on the submedian area on each side, and a few on the median area; some pores widely spaced anterior to the anal opening. The number of loculi in the disc pores usually varies from 5 to 12, however, quinquelocular disc pores are the most prevalent, especially in association with spiracles and on the posterior part of the abdomen, those segmental groups or rows anterior to the genital opening are the largest and have the most loculi.

Adult Male (fig. 5).—The adult males vary in size from 1 mm. to 1.5 mm. long and 0.4 mm. to 0.6 mm. wide; have a well-developed head (fig. 5C) bearing 10 eyespots, which are located on a prominent, heavily sclerotized plate which completely encircles the head in the central region except for a small, mediodorsal area which does not appear to be fused in mounted specimens; have one pair of 10-segmented antennae covered with setae, with segment 3 usually longest and the distal segments becoming progressively shorter; have a heavily sclerotized thorax bearing one pair of weakly-veined wings (fig. 5F) which are covered with spicules, and one pair of halteres (fig. 5B) which terminate in a somewhat basally swollen filament; have five-segmented legs bearing many setae, with the trochanter the shortest segment and bearing six sensory pits, three on each side, similar to those found on the trochanter of the female, the tibia bearing one pair of stout, spine-like setae on the anteroventral surface, with the tarsus (fig. 5D) bearing a pair of knobbed digitules and a tooth on the distal, plantar surface; have the eighth abdominal segment distinctive (fig. 5A), bearing two pairs of large setae which originate in deep pockets in the derm; have the abdomen terminating in a blunt, aedeagal sheath (fig. 5A) which has a ventral groove for reception of the aedeagus, the latter compressed laterally and sword-shaped.

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THE NERVOUS SYSTEM OF CERTAIN ABDOMINAL SEGMENTS OF THE CECROPIA LARVA (LEPIDOPTERA: SATURNIIDAE)[1]

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ABSTRACT

The muscles of the second and third abdominal segments and their innervations are described. The musculature of the third segment conforms, in general, to the pattern found in other lepidopterous larvae. In the second segment, which has no proleg, there are no muscles homologous with the retractors of the planta nor is there a branch of the ventral nerve root such as innervates these muscles in the third segment. This supports the theory that the proleg is a true metamorphic character, without phylogenetic significance. Also, the dissimilar musculature of the proleg in Cecropia as compared with other larvae supports Hinton's theory of the polyphyletic origin of prolegs in the Lepidoptera. Dorsal, ventral, and transverse pairs of nerve roots arising from each segmental ganglion seem homologous with those described for the pregenital segments of certain Orthoptera. Here, as in those Orthoptera, the ventral nerve fuses with the transverse nerve of its own ganglion, the dorsal nerve with the transverse nerve of the preceding segmental ganglion, and the spiracular muscles are innervated from the connective between the dorsal and the transverse nerves. These criteria of homology in such widely separated orders as Orthoptera and Lepidoptera support the concept of a basic segmental nerve pattern within the Hexapoda. The presence of these criteria of homology implies that holometabolous larvae, such as that of Cecropia, probably evolved from the hemimetabolous immature form, such as that of the orthopterans.

The assumption that at some time in the past history of the Hexapoda the abdominal segments, as arthropod leg-bearing somites, had essentially the same structure as the primitive thoracic and gnathal segments had led to the concept of an underlying homology of segmental musculature. Previous work based upon this concept supplied important evidence on the evolution of the insect thorax and appendages. Therefore, in a morphological study of the insect abdomen and its appendages, an attempt must be made to determine the presence of a basic plan of organization, as we have reason to believe exists in the cephalic and thoracic regions.

The concept of a basic plan of segmental musculature implies the presence of a basic primitive pattern of nerves to these serial muscles. If such a basic plan of homologous segmental musculature and innervation were present in each segment of this ancestor, the nerves innervating the segmental muscles of the insect would present a picture of the modifications of the basic primitive innervation pattern. As the essential purpose of the nerves is to transmit impulses, it would seem that selective pressures during the evolution from a primitive form to the present insect form would be of a lesser magnitude upon the nerves than upon the structures served by these nerves. A profound change in body structure might arise from a shift of the origin or attachment of a muscle group within the segment, while the corresponding change in the nerve branch innervating that muscle might result in a slight shift in the position at which the nerve branch passes from its ganglionic "root".

Many individual studies of the musculature and the ventral nerve cord of lepidopterous larvae have been carried out by various workers. Among these works only a few are sufficiently thorough to be of value in the establishment of homologies of nerves and muscles within the larval and adult stages of the same insect, as well as within different families of the order Lepidoptera and among different orders of insects. The lack of papers of this nature is due chiefly to the difficulty in recognizing homologies. Certain "landmarks" are of value in the establishment of homology. One such important landmark in the study of the insect abdomen is the spiracles. The winged imaginal stage of insects has brought about shifts of position in the thoracic spiracles of these forms, but the abdominal spiracles are believed to have retained a more primitive position within their respective segments, due to lesser selective pressure on them. Therefore, it would seem that the musculature and its innervations serving the abdominal spiracles would retain positions not far removed from that of the basic primitive segmental plan. Schmitt (1954) makes use of landmarks in his study of the nervous system of the pregenital abdominal segments of some Orthoptera. The segmental nerve patterns of the second and third abdominal segments of the Cecropia larva are compared in figures 5–7 with the nerve patterns of the third abdominal segments of *Dissosteira carolina* and *Acheta assimilis*, as presented by Schmitt (1954).

The nature of the abdominal legs of holometabolous larvae has long been a subject of controversy among morphologists. Eastham (1930), in his study of the embryology of *Pieris rapae*,

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maintained that prolegs retained on their segments are true appendages. He drew this conclusion because the prolegs develop in the same manner as appendages of the head and thorax, have the same relation to their own somites, and each develops a musculature comparable to that of the thoracic limbs. Snodgrass (1954) places no phylogenetic significance in the holometabolous larva as the holometabolous larva has "gone its own way" in evolution and just the merest thread of connection exists between the very specialized larvae and more generalized imaginal stages of these higher orders of holometabola. He regards the prolegs of holometabolous larvae as true metamorphic characters, that is to say, they are structures temporarily assumed by the young insect to better suit it for its own purposes. He further holds that the prolegs have no counterpart in the adult evolution and are discarded at the transformation to the imago. Pryor (1951) has pointed out that similarity in structure of nonsegmented organs of locomotion, as the prolegs, is not necessarily a criterion of homology. He holds that there is as much resemblance between a caterpillar and an onycophoran or a tardigrade as between a caterpillar and *Corydalus*. The work of Hinton (1952, 1955) seems to substantiate further the views of Snodgrass and Pryor in that he brings forth the theory that the prolegs of lepidopterous larvae have

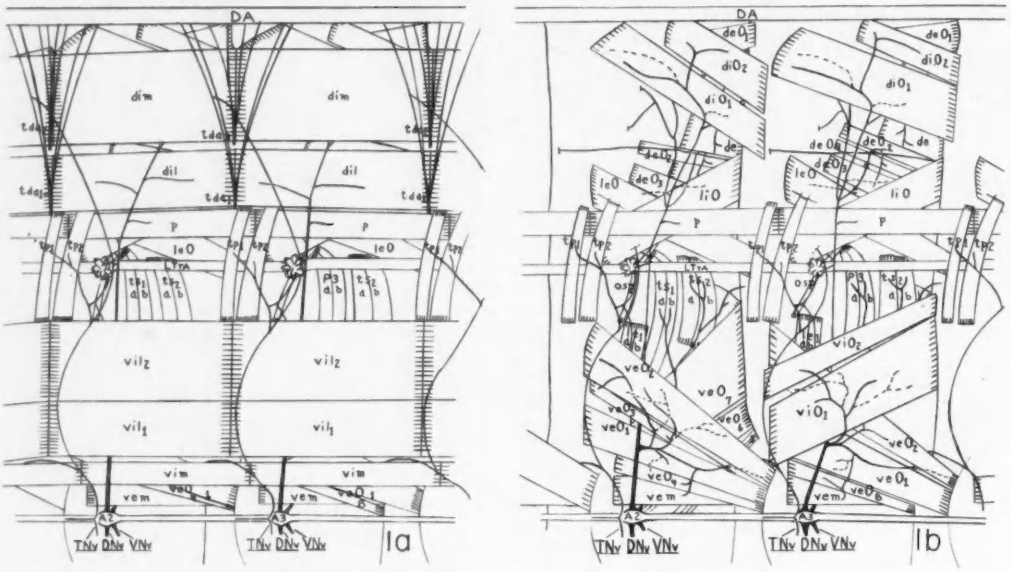


FIG. 1a.—Nerves and muscles of the right side of the second and third abdominal segments of the Cecropia larva. First stage of dissection. FIG. 1b.—Same, second stage of dissection.

ABBREVIATIONS USED ON THE FIGURES

Muscles

de, dorsal external
$deO_{1, 2, 3, \& 4}$, dorsal external oblique
dil, dorsal internal lateral
dim, dorsal internal median
$diO_{1 \& 2}$, dorsal internal oblique
dlsp, dilator of the spiracle
le, lateral external
$le_{1a \& 1b}$, lateral external
$le_{2, 3, \& 4}$, lateral external
leO, lateral external oblique
liO, lateral internal oblique
osp, occlusor of the spiracle
p, paratergal
P1, median group of abdominal leg
P2, 3_a, & 3_b, abdominal leg
P4 & 5, retractor of planta
P7, 8, & 9, abdominal leg
$tda_{1 \& 2}$, transverse dorsal alary
$tp_{1 \& 2}$, tergo-pleural
$ts_{1a, 1b, 2a, \& 2b}$, tergo-sternal
$ve_{1, 2, \& 3}$, ventral external
vem, ventral external median
$veO_{1, 2, 3, 4, 5, 6, 7, \& 8}$, ventral external oblique
$vil_{1 \& 2}$, ventral internal lateral
vim, ventral internal median
$viO_{1 \& 2}$, ventral internal oblique

Nerves

A2, ganglion of second abdominal segment
A3, ganglion of third abdominal segment
DNv, dorsal nerve
LNvD, longitudinal nerve of the dorsum
MdNv, median nerve
TNv, transverse nerve

Body Folds and Ridges

a, dorso-pleural line
b, proximal rim of principal segment of abdominal leg
c, mesal rim of principal segment of abdominal leg
Cx, coxa of abdominal leg
d, claws
e, point of insertion of the retractor muscles of the planta
Scx, subcoxa of abdominal leg
Sp, spiracle
Vs, planta or retractile vesicle

Miscellaneous

A–F, Upper case letters used to indicate points of homology
DA, dorsal aorta
integ., integument
LTra, lateral tracheal trunk
MVl, mid-ventral line
Tra, trachea

evolved independently at least eight times within the order Lepidoptera. In view of these theories very few substantiating accounts of the morphology of the lepidopterous prolegs can be found in the literature.

The writer expects in this study to shed some light on the nature of the abdominal proleg of the Cecropia larva by comparison of the musculature and its innervations in the nonproleg-bearing second abdominal segment with that of the proleg-bearing third abdominal segment of the Cecropia larva and with the nerve pattern of the third abdominal segment of *Dissosteira carolina* as presented by Schmitt (1954). This comparison may also shed some light upon the phylogenetic significance of the larva.

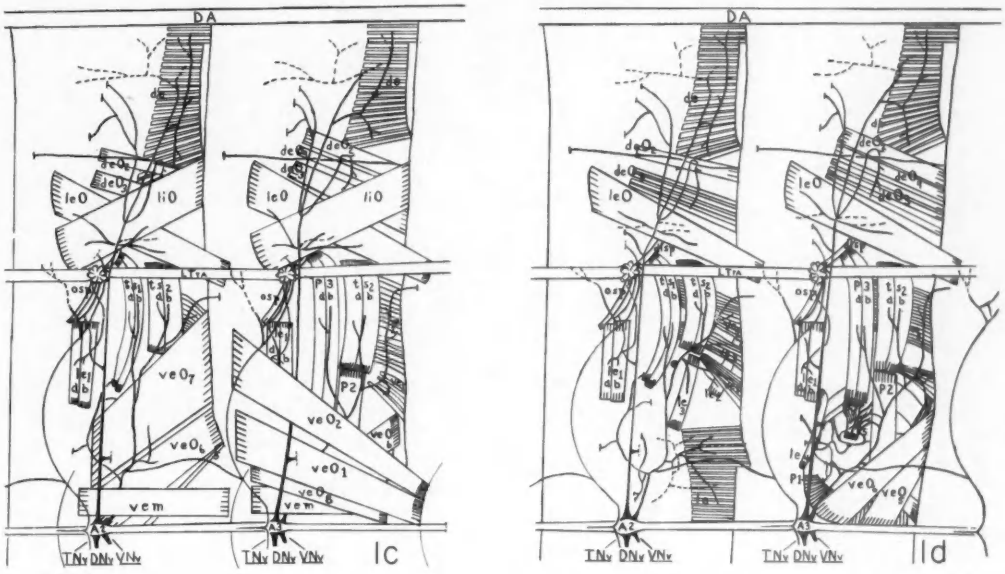


FIG. 1c.—Nerves and muscles of the right side of the second and third abdominal segments of the Cecropia larva. Third stage of dissection. FIG. 1d.—Same, fourth stage of dissection.

ACKNOWLEDGEMENTS

The writer wishes to express his gratitude to Dr. John B. Schmitt, Professor of Entomology, Rutgers University, for his guidance in selecting and carrying out this morphological study, and for his assistance in the preparation of this paper; to Dr. B. B. Pepper, Chairman, Department of Entomology, for his encouragement in continuing this basic problem; to Dr. C. C. Hamilton, Research Specialist in Entomology, for his aid in the photographic work. The writer is also indebted to Mr. Melville Osborne of Rahway, New Jersey, from whom the insect material was obtained.

METHODS OF NOMENCLATURE

The complexity of the musculature of the lepidopterous larva presents a problem of nomenclature. The nomenclature used in this study is based upon the general outline of body musculature set forth by Snodgrass (1931). This system provides sufficient flexibility for tentative designations of the complex musculature encountered in the lepidopterous larva. Some of the designations chosen might not be morphologically exact but were used for convenience, as is explained in the results wherever necessary.

The nomenclature of the nervous system follows that of Schmitt (1954). The large nerves or "nerve roots" leaving the segmental ganglion are named according to the general areas of the segment innervated by them. The nerve branches from these roots are indicated by the designations of the muscle groups which they innervate.

METHODS OF ILLUSTRATION

The illustrations of nerves and muscles are of two types. The first type might be termed "semi-perspective" in that an attempt has been made to present a reasonably true picture of the nerve-muscle relationships within the second and third abdominal segments and the abdominal proleg. The illustrations cannot be considered completely realistic, as some of the lines of the muscle groups indicated are represented as straightened and the nerve branch terminations in their muscles are only approximately indicated. Illustrations of the second type used in this study are diagrams of the nerves, which indicate the

spatial relationships of the nerves but which substitute lettered designations for the muscles innervated or the integument. This type of diagram is used by the writer as this study does not concern itself with the physiology of nerve endings but with the morphology of the nerve pattern as a guide in the establishment of homologies.

Points at which nerves pass but are not joined are represented by an interruption of the more laterad nerve, while nerve junctions are represented by uninterrupted lines. Nerve branches to muscle groups which have been removed are represented by broken lines.

RESULTS AND DISCUSSION

I. General

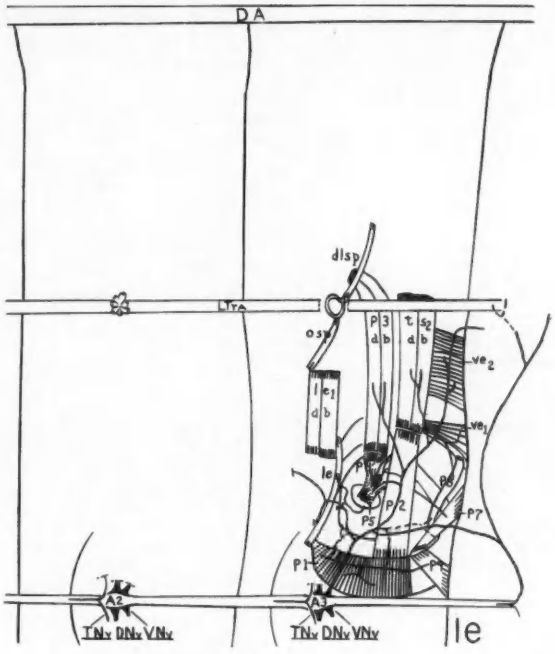
The motor nerves and musculature of the second and third abdominal segments were determined by "stage" dissections of the prepared larval specimens. It was found that by proceeding from the interior muscle layers to the exterior muscle layers upon the sub-hypodermal layer and the body wall, the study of the muscles

Table 1.—Summary of the classification of the musculature of several lepidopterous larvae (data, except that of Snodgrass and Libby, from Forbes, 1914)

Forbes	Lyonet	Lubbock	Berlese	Snodgrass	Libby
Longitudinal Dorsal					
Rectus	A, B, & C	1, 2, & 3	VII	dim & dil	
Segmental	D & G	4 & 5	VII		diO_1 & diO_2
From antecosta, oblique	F(4) & H	8 & 7	X		liO & leO
From antecosta to antecosta	E	6	IX	p	
From precosta	I & L	9, 10, & 11	XI		$deO_{2, 3, \& 4}$
From intercosta	Q & R	12 & 15	XVI	de	deO_1
Longitudinal Ventral, Supraneural					
Rectus	c, b, & d(3)	18, 17, & 16	2		$vil_{1 \& 2}$
Antecostal, oblique	f' (in *Malacosoma* only)				
Longitudinal Segmental	e & ff	20 & 19	2		$viO_{1 \& 2}$
To antecosta of following segment	f	25	IV		veO_2
From antecosta, oblique	h	+			veO_4
Longitudinal Ventral, Subneural					
Antecosta to antecosta, longitudinal	a & i	21 & 22	III	vim & vil	
To antecosta of following segment, oblique	g	24	IV		veO_1
Segmental, oblique	g'	25	2		veO_8
From front of leg	k	27	2		veO_6(part)
From near midventral line, between legs	p	28–30	1a		$veO_{6 \& 8}$
From posterior side of leg	t	57	V		P7, 8, & 9
From leg toward midventral line	x	56, 58	1a (1)	1	P1
From near midventral line to leg	(p')	46 (part)	1a		veO_6(part)
Spiracular	M	45		dlsp	
Transverse Supratracheal					
Acrosternal	θ	35	XVII		tp_1
At precosta	θ (2)	36	XVII		tp_2
Transverse Subtracheal, Above subventral fold					
From near incisure to precosta	α	37, 38	XVIII		
Mesotergite to mesosternite	δ, ϵ	51, 52	XVIIIa		$ts_{2a \& b}$
Crossing the pleurosternal line					
Spiracle to precosta	1	39	5b	osp	
Propleurite to precosta	m (sometimes)	42	5b		le_{1b}
	q (rarely)	40, 41			le_{1a}
Mesotergite to parts of leg	β, γ	46–50	5a, 5	3	P3a & b
Short posterior muscles	ζ, y	33–34	XVIII		$ve_{1 \& 2}$
Below the pleurosternal line					
Behind precosta	q, m	40, 41 (42)	5b		$le_{1a \& b}$
Across leg in front	n	43	6		le_4
Across leg behind (from ψ)	r	53–54	6	2	P2
From fold or ψ to leg	γ (part)		6a	5 & 6	P5
From fold or ψ to anterior edge of following segment	ζ (part)	31–32			P7, 8, & 9
	z	55			

and their innervations could be most readily facilitated (figs. 1a-e). The musculature thus discovered was then compared with the work of Forbes (1914), and the designations were added to those in his table of nomenclature. Table 1 presents a summary, based on Forbes, of the designations previously used for the musculature of several lepidopterous larvae and incorporating those used by the writer. The motor nerves were followed from their "roots" arising from the segmental ganglia to their terminations in muscles or upon the integument (figs. 1a-e). The individual nerve roots were diagrammed as the study progressed (figs. 3, 4).

ganglion of the Cecropia larva. The anterior lateral nerve arising from the segmental ganglion is designated the dorsal nerve DNv). The posterior lateral nerve arising directly from the ganglion is designated the ventral nerve (VNv). A median nerve (MdNv) is seen to arise at the separation of the interganglionic connectives anterior to the ganglion of the posterior segment. The median nerve gives rise to the transverse nerves (TNv) which pass laterally from the median nerve just anterior to the posterior segmental ganglion. The segmental ganglion and its lateral nerves are covered with a continuous nucleated sheath, the neurilemma. The portions



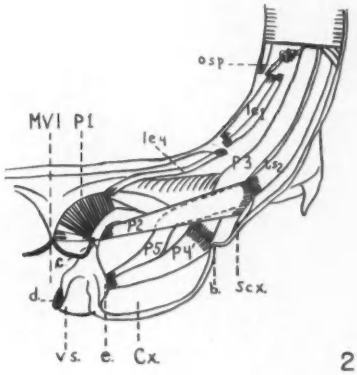


FIG. 1e.—Nerves and muscles of the right side of the second and third abdominal segments of the Cecropia larva. Fifth stage of dissection. FIG. 2.Posterior view of right abdominal proleg of the Cecropia larva.

The ventral nervous system consists of the postoral series of segmental ganglia and their connectives, constituting the ventral nerve cord (Snodgrass 1935). This study was concerned only with the portions of the ventral nerve cord and its lateral nerve roots within the second and third abdominal segments. The segmental ganglion (A2, A3) is an oval mass of nerve tissue, continuous anteriorly and posteriorly with the interganglionic connectives. The interganglionic connectives of the Cecropia larva are fused as they leave the ganglion posteriorly, and separate just anterior to their connections with the posterior segmental ganglion. Two lateral nerves and a median nerve arise from each segmental

of the ventral nervous system related to the second and third abdominal segments of the Cecropia larva are diagrammed in figure 1a-e.

II. The Dorsal Nerve.

The anterior nerve root from each of the abdominal segmental ganglia is herein designated the dorsal nerve (figs. 1a-d, 3). The dorsal nerve passes above the ventral external medial muscles and the ventral internal medial longitudinal muscles. The dorsal nerve then passes beneath the ventral internal lateral longitudinal muscles and passes over the tergo-sternal muscles (tsla-b; P3 a-b) and the lateral tracheal trunk just posterior to the spiracle. A short connective branch

Table 2.—Muscles innervated by the dorsal nerve of the second abdominal segment

Muscle	Symbol	Origin (or attachment)	Insertion (or attachment)
Dorsal external	de	Intercosta	Posterior intersegmental fold
Dorsal external oblique 1	deO_1	Intercosta	Posterior intersegmental fold
Dorsal external oblique 2	deO_2	Precosta	Posterior intersegmental fold
Dorsal external oblique 3	deO_3	Precosta	Posterior intersegmental fold
Dorsal internal lateral	dil	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal internal median	dim	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal internal oblique 1	diO_1	Antecosta	Posterior intersegmental fold
Dorsal internal oblique 2	diO_2	Precosta	Posterior intersegmental fold
Dilator of the spiracle	dlsp	Lateral wall of tergum dorsad of the spiracle	Atrium of spiracle
Lateral external 1a	le_1[a]	Dorso-pleural line	Sterno-pleural line
Lateral external 1b	le_1[b]	Dorso-pleural line	Sterno-pleural line
Lateral external oblique	leO	Antecosta	Antecosta
Lateral internal oblique	liO	Antecosta	Posterior intersegmental fold
Occlusor of the spiracle	osp	Mesal rim of atrium of the spiracle	Dorso-pleural line
Paratergal	p	Antecosta	Antecosta
Ventral external median	vem	Below antecosta	Antecosta of posterior segment
Ventral external oblique 1	veO_1	Above antecosta	Antecosta of posterior segment
Ventral external oblique 2	veO_2	Above antecosta	Antecosta of posterior segment
Ventral external oblique 3	veO_3	Above antecosta	Intersegmental fold of posterior segment
Ventral external oblique 4	veO_4	Below antecosta	Antecosta of posterior segment
Ventral internal lateral 1	vil_1	Anterior intersegmental fold	Posterior intersegmental fold
Ventral internal lateral 2	vil_2	Anterior intersegmental fold	Posterior intersegmental fold
Ventral internal median	vim	Antecosta	Antecosta

Table 3.—Muscles innervated by the dorsal nerve of the third abdominal segment

Muscle	Symbol	Origin (or attachment)	Insertion (or attachment)
Dorsal external	de	Intercosta	Posterior intersegmental fold
Dorsal external oblique 1	deO_1	Intercosta	Posterior intersegmental fold
Dorsal external oblique 2	deO_2	Precosta	Posterior intersegmental fold
Dorsal external oblique 3	deO_3	Precosta	Posterior intersegmental fold
Dorsal external oblique 4	deO_4	Precosta	Posterior intersegmental fold
Dorsal internal lateral	dil	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal internal median	dim	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal internal oblique 1	diO_1	Antecosta	Posterior intersegmental fold
Dorsal internal oblique 2	diO_2	Precosta	Posterior intersegmental fold
Dilator of the spiracle	dlsp	Lateral wall of tergum dorsad of the spiracle	Atrium of spiracle
Lateral external 1a	le_{1a}	Dorso-pleural line	Sterno-pleural line
Lateral external 1b	le_{1b}	Dorso-pleural line	Sterno-pleural line
Lateral external oblique	leO	Antecosta	Antecosta
Lateral internal oblique	liO	Antecosta	Posterior intersegmental fold
Occulusor of the spiracle	osp	Mesal rim of atrium of the spiracle	Dorso-pleural line
Paratergal	p	Antecosta	Antecosta
Ventral external median	vem	Below antecosta	Antecosta of posterior segment
Ventral external oblique 1	veO_1	Above antecosta	Antecosta of posterior segment
Ventral external oblique 2	veO_2	Above antecosta	Antecosta of posterior segment
Ventral external oblique 8	veO_8	Above antecosta	Posterior intersegmental fold
Ventral internal oblique 1	viO_1	Antecosta	Posterior intersegmental fold
Ventral internal oblique 2	viO_2	Antecosta	Posterior intersegmental fold
Ventral internal lateral 1	vil_1	Anterior intersegmental fold	Posterior intersegmental fold
Ventral internal lateral 2	vil_2	Anterior intersegmental fold	Posterior intersegmental fold
Ventral internal median	vim	Antecosta	Antecosta

runs from the dorsal nerve, fusing with the transverse nerve of the median system just posterior to the spiracle. This has previously been shown by Lyonet (1762), DuPorte (1915), and Swaine (1921).

The dorsal nerve continues to pass toward the middorsal region of the segment, a small branch passing to the integument just dorsad of the spiracle. The dorsal nerve then passes above the lateral internal oblique muscle and a branch passes anteriorly from the dorsal nerve passing above the lateral internal oblique muscle and beneath the paratergal muscle.

The dorsal nerve then passes above the paratergal muscle where a branch is seen extending anteriorly from the dorsal nerve and passing under the dorsal internal lateral longitudinal muscles. A branch also arises from the dorsal nerve root above the paratergal muscle, which passes posteriorly to innervate the paratergal muscle. Next the dorsal nerve passes obliquely posteriorly over the dorsal internal lateral longitudinal muscles and sends anterior and posterior branches which innervate this muscle group. The dorsal nerve then passes beneath the dorsal internal medial longitudinal muscles. The preceeding discussion is illustrated in figure 1a.

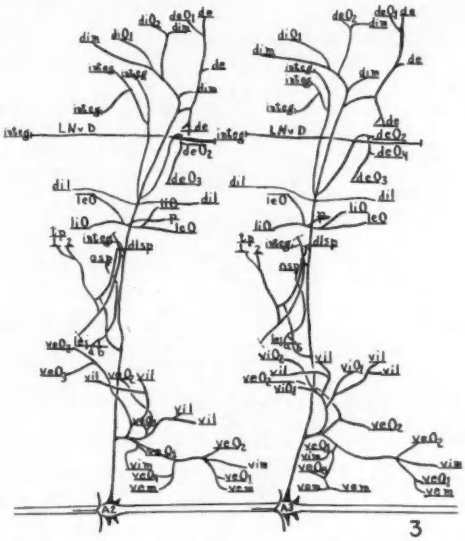
The dorsal and ventral internal longitudinal muscles and the paratergal muscle were then removed to allow further study of the dorsal nerve (fig. 1b).

Upon removal of the ventral internal longitudinal muscles the dorsal nerve is seen to pass over ventral external oblique muscles 1, 4, and 8 and beneath ventral external oblique muscles 2 and 3. The third abdominal segment also has two ventral oblique muscles which lie diagonally above the ventral external oblique muscles. The fact that these ventral internal oblique muscles are not homologous with the ventral external oblique muscle group 7 of the second abdominal segment is borne out by their innervations.

A large ventral branch arises from the dorsal nerve above ventral external oblique muscle 1. This branch passes posteriorly in the segment, sending out smaller branches which innervate the ventral internal lateral longitudinal muscles and many of the ventral external oblique muscles. The first nerve branch to arise from the ventral posterior branch of the dorsal nerve passes distally above the ventral external oblique muscles 2 and 3 and innervates these muscles and the ventral internal lateral longitudinal muscles of the second abdominal segment. The corresponding branch in the third abdominal segment innervates the ventral internal oblique muscles 1 and 2 and the ventral internal lateral longitudinal muscles.

The second nerve branch to arise from the ventral posterior branch of the dorsal nerve also innervates ventral external oblique muscles 2 and 3 and the ventral internal lateral longitudinal muscles of the second abdominal segment. The corresponding nerve branch in the third abdominal segment innervates the ventral external oblique muscle 2 as in the second abdominal segment.

The third nerve branch to arise from the ventral posterior branch of the dorsal nerve in the second abdominal segment passes medially above ventral



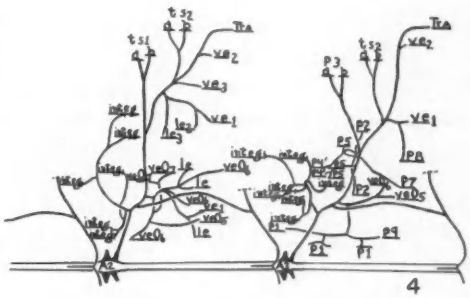


FIG. 3.—Diagram of the dorsal nerve roots of the second and third abdominal segments of the Cecropia larva.
FIG. 4.—Diagram of the ventral nerve roots of the second and third abdominal segments of the Cecropia larva.

external oblique muscle 1 and its branches innervate this muscle and the ventral internal medial longitudinal muscle. A fourth nerve branch from the ventral posterior branch of the dorsal nerve also passes medially above the ventral external oblique muscles 1 and 4 and the ventral external muscle innervating these muscles. In the third abdominal segment the third nerve branch to arise from the ventral posterior branch of the dorsal nerve passes medially above the ventral external oblique muscles 1 and 8, as well as the ventral external muscle. This nerve branch innervates these muscles, as well as the ventral internal medial longitudinal muscle. Therefore, it appears that the third and fourth nerve branches of the ventral posterior branch of the dorsal nerve in the second abdominal segment may be homologous with the third medial branch of the ventral posterior branch of the dorsal nerve in the third abdominal segment. If this were the case, one would conclude that the ventral external oblique muscle 4 of the second abdominal segment would be homologous with ventral external oblique muscle 8 of the third abdominal segment, the latter muscle having undergone a shift in its insertion from the precosta of the fourth abdominal segment to the posterior intersegmental fold of the third abdominal segment.

The ventral posterior nerve branch of the dorsal nerve continues to pass posteriorly above ventral external oblique muscle 1 until it reaches the posterior intersegmental fold, where medial and distal branches arise which innervate the ventral external oblique muscles 1 and 2. A fine branch continues to pass posteriorly from this fork and terminates at the insertion of the ventral internal medial longitudinal muscle (fig. 1b).

The removal of the dorsal internal lateral longitudinal muscles and the dorsal internal medial muscles allows one to pursue further the innervation of the dorsal area of the segment.

The dorsal nerve is then observed to pass over the dorsal internal oblique muscle just distad to the paratergal muscle, and continues to pass dorsally and somewhat posteriorly above the dorsal external oblique muscles 2 and 3. The dorsal nerve forks just medial of the dorsal internal oblique muscle 1. One of these branches passes above the dorsal internal oblique muscles 1 and 2 and innervates these muscles, as well as the dorsal internal medial longitudinal muscle group. The other branch of this fork passes beneath the dorsal internal oblique muscles 1 and 2 and innervates the dorsal external muscles and the dorsal external oblique muscle group 1 (figs. 1d and 1c).

Table 4.—Muscles innervated by the ventral nerve of the second abdominal segment

Muscle	Symbol	Origin (or attachment)	Insertion (or attachment)
Lateral external	le	Posteriorly on sternum	Posterior intersegmental fold
Lateral external 2	le_2	Posteriorly latero-dorsal	Sterno-pleural line
Lateral external 3	le_3	Dorso-pleural line mesad of (ts_{2b})	Sternum anterior to (le)
Tergo-sternal 1a	ts_{1a}	Paratergal wall posterior to and above the level of the spiracle	Sterno-pleural line
Tergo-sternal 1_b	ts_{1b}	Paratergal wall posterior to and above the level of the spiracle	Sterno-pleural line
Tergo-sternal 2a	ts_{2a}	Paratergal wall posterior to (ts_{1b})	Dorso-pleural line distad of (P2)
Tergo-sternal 2_b	ts_{2b}	Paratergal wall posterior to (ts_{2a})	Dorso-pleural line posterior to (ts_{2a}) and distad of (P2)
Ventral external 1	ve_1	Sterno-pleural line posterior to (ts_{2b})	Posterior intersegmental fold
Ventral external 2	ve_2	Mesad of spiracular line laterad of (ts_{1b})	Posterior intersegmental fold
Ventral external 3	ve_3	Sterno-pleural line mesad of (ts_{1b})	Posterior intersegmental fold
Ventral external oblique 5	veO_5	Mid-ventral line	Posterior intersegmental fold
Ventral external oblique 6	veO_6	Precosta	Posterior intersegmental fold
Ventral external oblique 7	veO_7	Precosta	Posterior intersegmental fold

Just distad to the paratergal muscle, two fine nerve branches arise from the dorsal nerve, both passing dorsally and parallel to the dorsal nerve. Each of these nerve branches fuses with the longitudinal nerve of the dorsum above the dorsal external oblique muscle groups 2 and 4. This fusion is indicated in the works of Lyonet (1762), DuPorte (1915), and Swaine (1921). The anterior branch sends branches to the sub-hypodermal layer. The posterior branch innervates dorsal oblique muscles 2, 3, and 4.

The longitudinal nerve of the dorsum is present in each abdominal segment studied. This nerve is segmental in length and has its anterior attachment on the integument at the base of the dorsal internal lateral longitudinal muscles and its posterior attachment on the posterior intersegmental fold beneath the insertion of the lateral internal oblique muscles (fig. 1b).

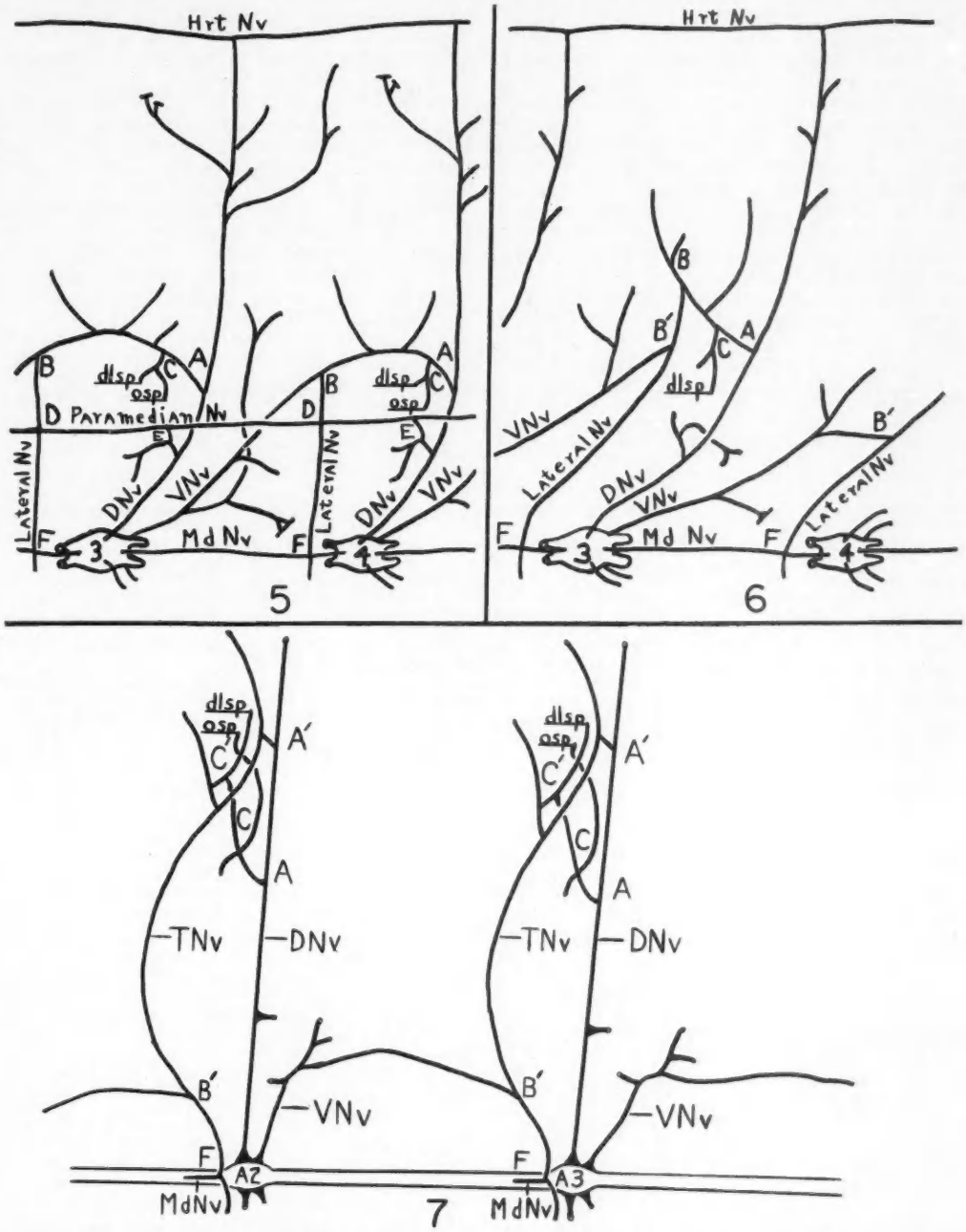


FIG. 5.—Diagrams of the nerve patterns of the right side of typical abdominal segments of *Dissosteira carolina* (after Schmitt 1954), with points of homology indicated. Mesal aspect. FIG. 6.—Same, *Acheta assimilis* (after Schmitt 1954). FIG. 7.—Same, Cecropia larva.

Upon removal of the paratergal muscle a short connective nerve branch from the dorsal nerve, connected to a nerve branch which passes beneath the paratergal muscle perpendicular to the dorsal nerve, is observed to branch and innervate the lateral internal oblique and lateral external oblique muscles (fig. 1c).

To complete the study of the dorsal nerve, ventral internal oblique muscles 1 and 2 and ventral external oblique muscles 1–5 and 8 were removed. This exposed the ventral anterior branch of the dorsal nerve.

The ventral anterior branch of the dorsal nerve arises from the dorsal nerve above the sterno-pleural line. This nerve branch passes anteriorly above the lateral external muscles 1a-b, and at this point it branches. One of its branches innervates lateral external muscles 1a-b, and the other branch passes dorsally and branches again. The anterior nerve of this fork connects with a branch of the transverse nerve which innervates the dilator of the spiracle. The posterior nerve of this fork innervates the occlusor of the spiracle (fig. 1d).

The ventral anterior branch of the dorsal nerve which connects with the transverse nerve exhibits several points of similarity with the dorsal nerve of abdominal segments of the orthopteran *Dissosteira carolina* (Schmitt 1954). The point at which the ventral anterior branch leaves the dorsal nerve is designated "A". The connection of the ventral anterior branch of the dorsal nerve with the transverse nerve, from which a nerve branch innervates the dilator of the spiracle, is designated "C" (fig. 7). The point at which the nerve branch to the dilator of the spiracle leaves the connective between the dorsal and transverse nerves is designated "C'" (fig. 7). The establishment of these homologies in the nerve patterns of the *Cecropia* larva and *Dissosteira carolina* lends evidence to the concept of the presence of a basic segmental plan of nerves. These homologies also imply that the holometabolous larva might have developed from a hemimetabolous immature form such as the Orthoptera nymph.

The muscles innervated by the dorsal nerve in the second and third abdominal segments are indicated in tables 2 and 3.

Table 5.—Muscles innervated by the ventral nerve of the third abdominal segment

Muscle	Symbol	Origin (or attachment)	Insertion (or attachment)
Median group of abdominal leg	P_1	Mid-line of the venter	Mesal rim of the base of the leg laterad of the mid-ventral line
Abdominal leg	P_2	Dorso-pleural ridge	Mesal rim of the principal segment of the leg
Abdominal leg	P_{3a}	Paratergal wall posterior to and above the level of the spiracle	Proximal rim of the principal segment of the leg
Abdominal leg	P_{3b}	Paratergal wall posterior to and above the level of the spiracle	Proximal rim of the principal segment of the leg
Retractor of the planta	P_4	Proximal rim of the principal segment of the leg	Inner surface of the planta
Retractor of the planta	P_5	Dorso-pleural ridge	Inner surface of the planta
Abdominal leg	P_7	Posterior intersegmental fold	Mesal rim of the principal segment of the leg distad of (P_6)
Abdominal leg	P_8	Dorso-pleural ridge	Posteriorly upon the proximal rim of the principal segment of the leg
Abdominal leg	P_9	Posterior intersegmental fold	Mesal rim of the principal segment of the leg posterior to (P_1) and (P_2)
Tergo-sternal 2a	ts_{2a}	Paratergal wall posterior to (ts_{1b})	Dorso pleural line distad of (P_2)
Tergo-sternal 2b	ts_{2b}	Paratergal wall posterior to (ts_{2a})	Dorso-pleural line posterior to (ds_{2a}) and distad of (P_2)
Ventral external 1	ve_1	Sterno-pleural line posterior to (ts_{2b})	Posterior intersegmental fold
Ventral external 2	ve_2	Mesad of spiracular line laterad (ts_{1b})	Posterior intersegmental fold

III. The Ventral Nerve.

The posterior nerve root from each of the abdominal segmental ganglia is herein designated the "ventral nerve" (figs. 1a-e, 4). The ventral nerve leaves the ganglion and passes obliquely posteriorly beneath the ventral external medial muscle and ventral external oblique muscles 1, 2, 3, 4, and 8. Removing these muscle groups, the ventral nerve of the second abdominal segment passes over ventral external oblique muscles 6 and 7. The ventral nerve of the third abdominal segment also passes over ventral external oblique muscle 6.

The first branch arising from the ventral nerve is an anterior branch which branches to innervate the subhypodermal layer of the integument in

the sternal region of the second abdominal segment. The corresponding branches of the anterior branch of the ventral nerve in the third abdominal segment innervate the mesal and proximal rims of the coxa of the proleg. A branch of this nerve also innervates the inner surface of the planta.

The second branch arising from the ventral nerve passes posteriorly above the ventral external oblique muscle 6, crossing the posterior intersegmental fold from beneath ventral external oblique muscle 2. This nerve branch continues posteriorly into the posterior segment where it connects with the transverse nerve. This has previously been observed in Lepidoptera by DuPorte (1915) and Swaine (1921). The point of connection of this posterior branch of the ventral nerve with the transverse nerve is designated point "B" and provides a useful "landmark" (fig. 7). Schmitt (1954) indicates this point "B" as an important "landmark" in Orthoptera.

external muscles of the second abdominal segment may be homologous with proleg muscle groups 1 and 9 of the third abdominal segment.

The ventral nerve continues to pass obliquely posteriodorsally above lateral external muscle 3 of the second abdominal segment and proleg muscle 2 of the third abdominal segment. A branch of the ventral nerve arises in the third abdominal segment and passes laterad to innervate proleg muscle groups 4 and 5. Neither this nerve branch nor these muscle groups were present in the second abdominal segment. The ventral nerve branches, the anterior branch passing to tergo-sternal muscles 1a-b of the second abdominal segment and the proleg muscles 3a-b of the third abdominal segment. These muscle groups appear to be homologous. A fine branch arises at this fork in the ventral nerve in the third abdominal segment and passes beneath proleg muscle 2 innervating this muscle and proleg muscles 4, 5, and 7.

The posterior branch of the fork of the ventral

Table 6.—Muscles of the second and third abdominal segments innervated by the transverse nerve

Muscle	Symbol	Origin (or attachment)	Insertion (or attachment)
Dilator of the spiracle	dlsp	Lateral wall of tergum dorsal of the spiracle	Atrium of the spiracle
Occlusor of the spiracle	osp	Mesal rim of the spiracle	Dorso-pleural line
Transverse dorsal alary 1	tda_1	Intersegmental fold between (p) and (dil) just anterior to (tp_1)	Dorsal aorta
Transverse dorsal alary 2	tda_2	Intersegmental fold between (dil) and (dim)	Dorsal aorta
Tergo-pleural 1	tp_1	Intersegmental fold between (p) and (dil)	Intersegmental fold just distad of (vil_2)
Tergo-pleural 2	tp_2	Dorsum below antecosta and between fibers of (leO)	Antecosta just distad of (vil_2)

The ventral external oblique muscles 5, 6, and 7 of the second abdominal segment and ventral external oblique muscles 5 and 6 of the third abdominal segment were then removed. Another posterior branch of the ventral nerve was then observed to run posteriorly in the sternal area of each segment. This posterior branch runs laterad of the posterior ventral nerve branch which connects with the transverse nerve in the posterior segment.

The posterior nerve branch of the ventral nerve, observed upon removal of ventral external oblique muscles 5, 6, and 7, sends branches to innervate these muscle groups in the second and third abdominal segments. Other branches from this posterior nerve branch of the ventral nerve innervate the lateral external muscle group of the second abdominal segment (fig. 1d). What appeared to be the corresponding branches of this posterior nerve branch of the ventral nerve innervate proleg muscle groups 1 and 9 (fig. 1e). Therefore, it appears that the posterior lateral nerve passes obliquely posteriorly, sending branches to innervate lateral external muscles 2 and 3 and ventral external muscle 3 of the second abdominal segment, as well as proleg muscle 8 of the third abdominal segment. Branches also arise from the posterior branch of the fork of the ventral nerve, which innervate tergosternal muscles 2a-b and ventral external muscles 1 and 2 of both the second and third abdominal segments. The posterior branch of the fork of the ventral nerve passes posteriorly over the intersegmental fold just ventrad of the lateral tracheal trunk and innervates trachea from the spiracle of the posterior abdominal segment.

The muscles innervated by the ventral nerve in the second and third abdominal segments are indicated in tables 4 and 5.

IV. The Transverse Nerve.

The unpaired median nerve of each abdominal ganglion arises from the fused intersegmental ganglionic connectives at the point where the

connectives separate, a short distance anterior to the ganglion of the following segment. The median nerve of each of the abdominal segments considered in this study gives off a pair of transverse nerves, which run over the ventral and dorsal internal longitudinal muscles.

An important "landmark" occurs at point B, where the transverse nerve connects with a branch of the ventral nerve as previously stated in the discussion of the ventral nerve. The transverse nerve forks before reaching the spiracle. The anterior branch of this fork sends a branch which innervates tergopleural muscles 1 and 2 and a branch which connects with the anterior branch of the dorsal nerve and innervates the spiracular muscles. This branch provides points A, C, and C′ for "landmarks," as previously stated in the discussion of the dorsal nerve.

The posterior branch of the fork of the transverse nerve passes just posterior to the spiracle where it has a short connective with the dorsal nerve. The transverse nerve then passes obliquely anteriorly to innervate the transverse dorsal alary muscles on both sides of the intersegmental fold (fig. 1a).

The study of the nervous system of the silkworm, *Bombyx mori* Linné, by Kuwana (1932) has shown that the transverse nerve does not terminate with the branches which innervate the transverse dorsal alary muscles. He has shown that branches of the transverse nerve also pass with the transverse dorsal alary muscles and join the heart nerve.

The muscles innervated by the transverse nerve in the second and third abdominal segments are indicated in table 6.

V. The Proleg.

The innervation of the proleg has previously been treated in the discussion of the ventral nerve.

The musculature of the proleg of the Cecropia silkworm is somewhat different from that of *Malacosoma americana* as shown by Snodgrass (1931), or from several other lepidopterous larvae described by Hinton (1952, 1955). A possible explanation for the variation of proleg musculature among lepidopterous larvae is found in the theory presented by Hinton (1955), that a climbing type of proleg has been evolved no less than eight times within the Lepidoptera. He holds that the climbing type of proleg has been independently evolved in the Zygaenidae, Papilionoidea, Geometridae, Phalaenoidea, and Sphingidae, and several times in the series Bombycoidea-Saturnoidea.

The nomenclature used in this study of the abdominal proleg was adapted from Snodgrass (1931), with some modifications. Snodgrass (1931) refers to a retractor muscle 4 which arises on the body wall above the spiracle and inserts on the inner surface of the planta, and also a muscle 3 which arises above the spiracle and inserts on the proximal rim of the principle segment of the leg. The Cecropia larva has two muscle groups which arise on the body wall above the spiracle and insert on the proximal rim of the principal segment of the proleg ($P3_{ab}$, fig. 2), and a short retractor muscle group which arises on the proximal rim of the principal segment of the proleg and inserts on the inner surface of the planta (P4, fig. 2). No muscle 4 is present in the Cecropia larva. Snodgrass (1931) indicates muscles 5 and 6 present in *Malacosoma americana*, both of which arise on the dorso-pleural ridge and insert on the inner surface of the planta. The Cecropia larva possesses only one muscle group arising on the dorso-pleural line and inserting on the inner surface of the planta (P5, fig. 2).

The musculature of the right abdominal leg of a typical proleg bearing abdominal segment of the Cecropia larva viewed mesally is seen in a posterior view in figure 2.

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GROSS EXTERNAL MORPHOLOGY OF EMBRYOS OF CULEX TARSALIS COQUILLETT (DIPTERA: CULICIDAE)[1]

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ABSTRACT

A method is described for observing living mosquito eggs that have transparent shells. The gross embryology of *Culex tarsalis* Coq. is presented, accompanied by a series of diagrams showing growth phases and a time-table that lists when those phases occur at specific temperatures. The occurrence of blastokinesis in Culicidae is discussed.

The mechanical difficulties involved in sectioning mosquito eggs has discouraged workers from studying their embryology. The preovipositional development of the eggs, before the chorion has formed and hardened, has been investigated by Nath (1924), Nicholson (1921), Parks (1955), and others. Sectioning of eggs after oviposition has been done successfully, as reported in the literature, by only two investigators, Gander (1951) and Larsen (1952). Gross observations of unsectioned embryos after removal of the chorion have been recorded by DeCoursey and Webster (1952) and Telford (1957). The present work makes use of a method for studying living eggs of *Culex tarsalis* Coquillett, a mosquito that has a transparent shell which permits observation of the maturing embryo without subjecting the egg to rigorous procedures of shell removal. It is hoped that this study will be useful as a base for expanding research including experimental embryology on mosquito eggs.

MATERIALS AND METHODS

Eggs used for the study were obtained from a *C. tarsalis* colony, Bakersfield strain, maintained at the California Department of Public Health facility in Fresno.

A camera lucida attached to a compound microscope was used to make the diagrams.

Since no satisfactory fixative has been found for mosquito eggs, all observations were on live material. A few eggs were separated from each raft for observation at timed intervals after oviposition.

Although the exochorion is transparent, its irregular surface tended to obscure embryonic features, and its removal was helpful. Two methods were used to support the eggs for microscopic examination. For the first method, eggs were drained on absorbent paper, then submerged in a drop of peanut oil on a glass slide. The oil had a clearing effect on the exochorion. Most eggs collapsed in oil within a half-hour, after which further observations of embryonic development were impossible. Advantages of the oil were that it did not evaporate and it cushioned the eggs from vibrations. For the second method, eggs were exposed briefly to ether, which loosened the exochorion and thus facilitated its removal with dissecting pins. Observations were then made of the eggs in water. This method was used for continued observations of single embryos. Very brief exposure to ether had no adverse effect on the embryos.

Embryonic growth series were made from rafts maintained at three temperatures: 70°, 80°, and 90° Fahrenheit.

DESCRIPTION OF GROSS EMBRYOLOGY

The study here presented deals only with those gross external morphological features of *C. tarsalis* embryos that can be clearly seen in live eggs through a compound microscope. External shell structures have been omitted in the figures.

The egg is an elongated oval. It is convex on one side and evenly concave on the other when viewed laterally. The anterior part of the egg, which normally rests on the water surface, is the thicker, rounded end. The thinner, pointed, and more or less hooked end is posterior. Orientation of the diagrams is according to the final position of the embryo just prior to hatching, the dorsum of the embryo being on the convex side of the egg. Sizes of eggs are variable. There are slight differences in growth rates of embryos within single egg rafts, but hatching of all eggs in a raft is usually completed in 1 hour. The embryonic contents may or may not fill the entire shell.

The coloring of eggs is due to pigmentation in the endochorion. When oviposited the eggs are creamy white. The color progresses to yellowish, light gray, dark gray, then dark brown. Shells are fully darkened within 3 hours after oviposition. Expansion of the shells occurs rapidly during the darkening process, then continues gradually until time of hatching.

Embryonic growth stages at three temperatures are listed in table 1.

A newly laid egg contains a large yolk mass (fig. 1). Nuclear divisions and migration of cleavage nuclei cannot be seen in whole, live eggs.

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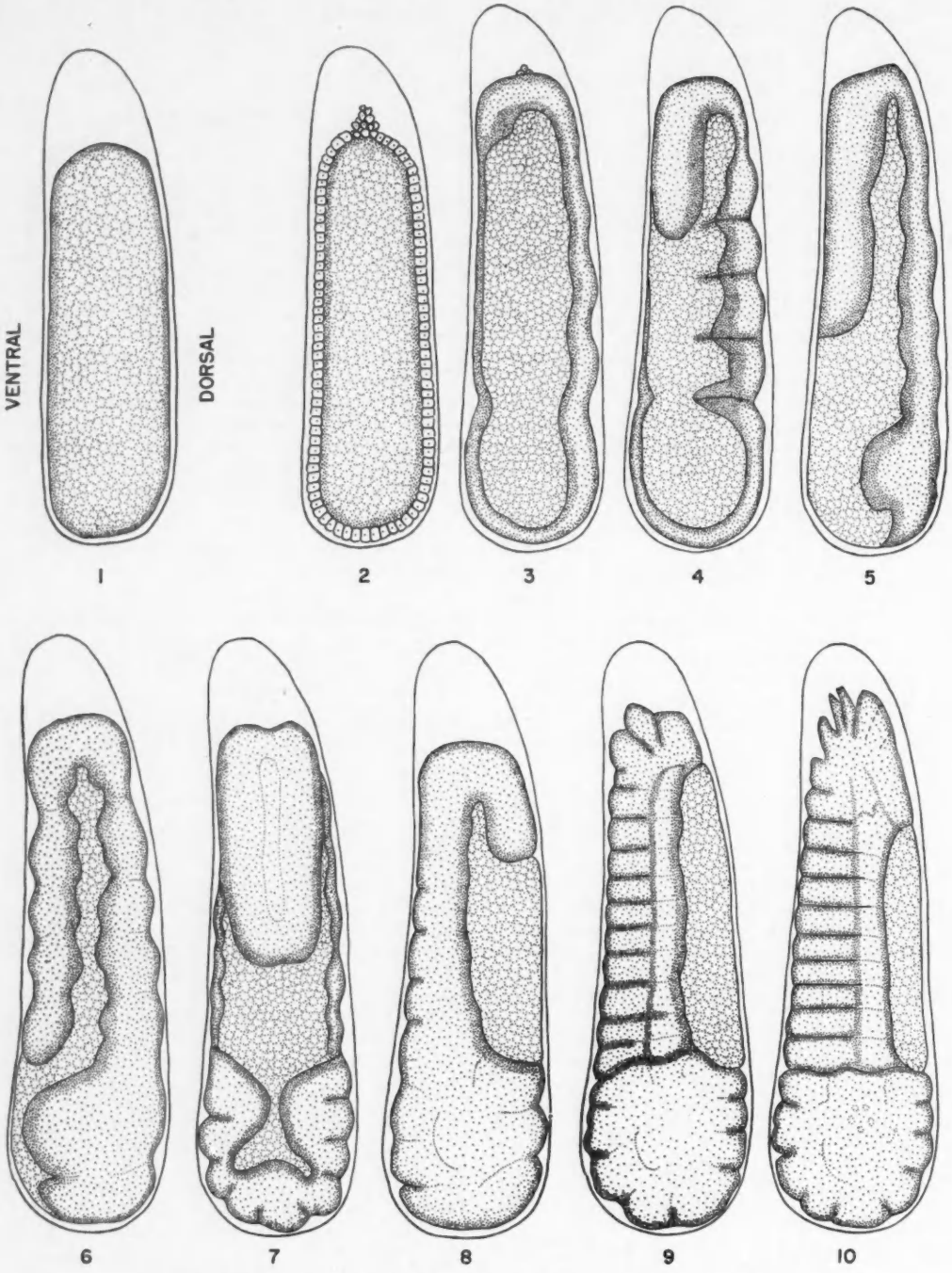
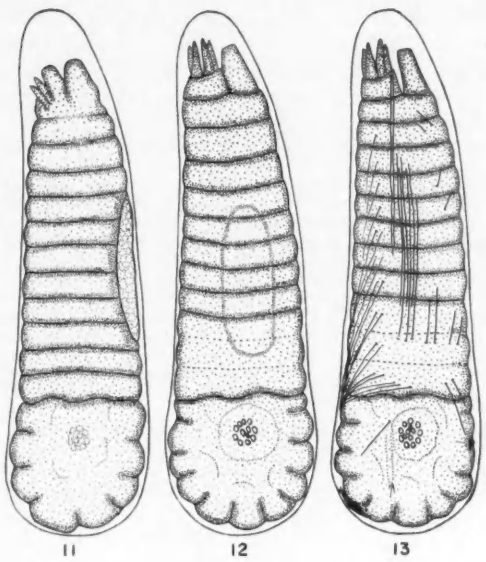


FIGS. 1 to 13.—Successive stages in embryonic development of *Culex tarsalis*. The various stages are identified and described in the text.



The cleavage nuclei become visible at the periphery of the yolk as the blastula forms. Although the blastoderm covers the entire surface of the yolk, it is clearly visible only at the edges where the light shines through the thinner layers. The single cell layer has a rough appearance during its early formation but soon smooths to form an even surface. Germ cells appear posteriorly at about the same time that the blastoderm is first seen (fig. 2). Unfertilized eggs often develop to a stage resembling the blastula. Wrinkles occurring in the blastoderm on the dorsal side of the egg represent the early beginnings of the germ band. At this time the germ cells sink back into the yolk (fig. 3). The blastoderm thickens dorsally as the germ band forms. The lateral cells appear to migrate to aid in formation of the germ band, and the ventral cells flatten to form the serosal membrane. A proliferation of cells creates more material than the embryonic rudiment can accommodate causing the formation of furrows which resemble superficial segmentation (fig. 4). The number of metameres and the shape of the germ band during this formative stage are variable, but there results an accumulation of embryonic substance on the dorsal side of the egg with the primary tail advancing on the ventral side (fig. 5). As the tail elongates, the furrows smooth out. The cephalic lobes grow over the surface of the yolk toward the ventral side of the egg. Growth continues until the caudal and cephalic ends of the developing embryo approach each other (fig. 6). Then the tail moves away from the head. When it has receded one-fourth to one-third of the distance, the embryo begins a 180-degree rotation about its longitudinal axis (fig. 7).

Table 1.—Timetable for *Culex tarsalis* embryonic growth stages

Stage	Hours		
	70° F.	80° F.	90° F.
Blastula	3–7	2–7	2–5
Wrinkles of early germ band	7–10	6–8	5–6
Superficial segments	9–11	7–9	6–7
Cephalic lobes, tail moving forward	11–18	7–10	6–9
Tail forward	17–26	8–14	7–13
Blastokinesis	25–29	14–17	13–15
Tail lobed	30–32	20–22	16–18
Appearance of eye	31–34	21–23	16–18
Completion of dorsal closure	44–52	27–35	22–25
Appearance of hatching spine	50–55	33–40	24–25
Hatching	61–68	43–48	30–33

After the embryo has revolved, the cephalic lobes fuse and segmentation of the body becomes evident. The tail rapidly recedes, and the lateral margins of the embryo grow around the yolk (fig. 8). Differentiation proceeds anteriorly and posteriorly from the prothorax: the body and head segments are clearly defined when the anal segment becomes lobed (fig. 9). At the time when rudimentary papillae are forming on the last abdominal segment, the eye can be vaguely discerned as a yellowish spot. A small yolk sac still remains (fig. 10). As the yolk sac becomes smaller, the yellow color of the eye changes to orange-red, and the caudal appendages become more distinct. The thoracic segments are not yet fused (fig. 11). Upon completion of the dorsal closure, no yolk is visible external to the embryo. The anal segment becomes complete with four papillae and an air tube, and the eye changes to dark red (fig. 12). Slight movements of the embryo may be detected.

The thoracic segments fuse about the time the hatching spine first appears as a dark smudge on the top of the head. Although the body hairs are present they are extremely light and do not become clearly visible until immediately before hatching. Lastly, the eye develops a very dark center with red edges, and the mouth brushes can be seen as coppery patches on the front of the head (fig. 13). With violent movements the embryo erupts from the shell.

DISCUSSION

The method described for observing embryogenesis is applicable only to those mosquito species that have transparent shells, such as *Anopheles*, *Culex* and *Culiseta*. The opacity of the thicker chorions of *Aedes*, *Psorophora*, and others, prevents light transmission through the shells.

Blastokinesis has not previously been recorded for mosquito embryos. Telford (1957), who worked with *Aedes dorsalis* (Meigen), and Larsen (1952), who worked with *Culiseta inornata* (Williston), saw nothing resembling a revolution in

slide material. Gander (1951) compared the early development of *A. aegypti* (Linnaeus) with that of *Sciara coprophila* (Lintner), which, according to DuBois (1932) and Butt (1934), does not revolve. The reorientation of the embryo after revolution was not detected in mounted material, either whole or sectioned. In live eggs it is readily seen in relation to the shape of the shell. The present author has watched blastokinesis in *C. tarsalis*, *C. quinquefasciatus* Say, *C. inornata*, and *Anopheles freeborni* Aitken. It has been observed in *A. nigromaculis* (Ludlow) after partial bleaching of the shells with hydrogen peroxide. About 1 hour at room temperatures is required for the 180° rotation.

Statements that the germ band forms on the ventral surface of the egg have been made by mosquito embryologists who were unaware of blastokinesis. The germ band which eventually becomes the ventral side of the embryo forms on the convex side of the egg. After revolving, the dorsum of the embryo is on the convex side. Orientation of the egg is easily established in respect to the egg tooth on the dorsum of the head of a mature embryo. Christophers (1945) described the concave side of *C. pipiens* Linnaeus and *C. molestus* Forskal eggs as dorsal. In his account of hatching, the egg cap remained attached to the shell at a mid-dorsal line which was located on the opposite side of the embryo from the egg tooth. At the time of hatching, as observed by the present author, the shell opens at the egg tooth, dorsally, and the cap is detached except for a small hinge mid-ventrally.

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SCIENTIFIC NOTES

The Courtship and Copulation of Pasimachus punctulatus Haldemann (Coleoptera: Carabidae)[1]

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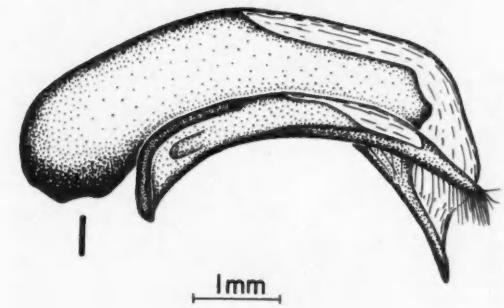
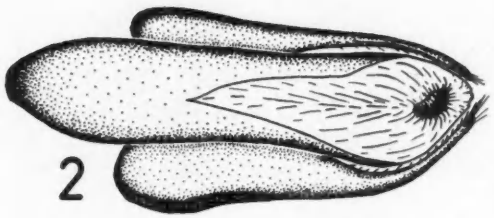
On July 9, 1957, while collecting at night with a headlamp in a ridge-top oak-hickory forest in Hocking County, Ohio, I observed the courtship and copulation of the large ground beetle, *Pasimachus punctulatus* Haldemann. Owing to the paucity of records concerning such observations and the increasing significance of behavior patterns associated with reproduction in insects—in species recognition as well as in evolutionary and comparative studies—the information seems worth recording.

My attention was initially attracted by a scuffling noise in the leaf litter, made by the male pursuing the female. Shortly after I turned my headlamp upon the insects, the male overtook the female and closed his mandibles around the constriction behind her pronotum. This constriction is particularly pronounced in members of this genus, and in this species the mandibles of the male are about twice as long as those of the female.





FIGURES 1 and 2.—Male genitalia of *Pasimachus punctulatus* Haldemann.
FIG. 1.—Lateral view of penis and left paramere.
FIG. 2.—Dorsal view of penis and both parameres.

For about 2 minutes the female struggled violently, dragging the male about through the leaves, but not succeeding in moving far from the spot where he had originally caught her. Eventually she slackened her struggle and the male, in some way which I could not perceive, instantly flipped her completely over on her back. He now lay beneath her, also on his back, his mandibles still fastened upon her thorax. When this happened the female stopped struggling and lay completely motionless. After a few seconds the male curled his abdomen up toward the tip of the female's abdomen and extruded his genitalia. Then for about 90 seconds he tapped lightly and rhythmically with both parameres upon the apical edge of her last abdominal sternite, his penis poised between the parameres just beyond the center of the tip of her abdomen. The parameres in this species are slender, blade-like, sclerotized structures bearing a comb-like row of long setae along their "tapping" (ventral) edges near the tips (fig. 1–2). The tapping rhythm was too rapid for accurate visual analysis, but it did not appear to be a simple steady sequence, and it may have been a series of pairs of taps, i.e., two closely spaced taps, a slightly longer interval, two closely spaced taps, a slightly longer interval, etc. The female's genital orifice was closed when this tapping began. Twice during the 90 seconds it opened slightly, but only momentarily, and both times the male darted the penis forward, but did not succeed in inserting it, and resumed the tapping of the parameres almost immediately. Finally, the female's genital orifice opened very obviously and the male inserted the penis and stopped tapping the parameres. The parameres remained outside and did not appear to function further. The insects remained attached for 2 or 3 minutes, with no movement visible other than a throbbing of the male's abdomen. At the end of this time the penis of the male slipped out and his genitalia were retracted and disappeared entirely. The insects lay motionless for about 2 minutes, then the female suddenly jumped up, and both ran off through the leaves.

It is significant that the parameres were never used as pries during the above activities, and the genitalia were not forced together, successful intromission of the penis depending upon what appeared to be a positive response by the female. This response was apparently a result of the prolonged and peculiar tapping of the parameres which should therefore be interpreted as a courtship pattern. It would be interesting to compare this part of the precopulatory behavior of this species with that of other species in this genus which occur in the same areas.

The sensory function of the parameres (styli) in beetles has already been pointed out by Jeannel (1941) who notes that they remain outside during copulation and are brought into contact with the perigenital integument of the female. He suggests that their tactile sensory effects upon the female are much more important in species isolation than are structural differences which might cause interspecific copulation to be mechanically impossible. He substantiates this suggestion by pointing out unusually large differences in the structure of the parameres in closely related, otherwise very similar species which live together. The present observations corroborate Jeannel's conclusions and further suggest that the titillatory function of the parameres may involve the rate or rhythm with which they are brought into contact with the female's abdomen in addition to the effects of their peculiarities of structure.

The activities described here were observed with a bright light only a few inches away, and the beetles were apparently not disturbed. Both specimens were captured and are now located in the University of Michigan Museum of Zoology. I am indebted to Dr. William C. Stehr of the Department of Zoology, Ohio University, Athens, for confirmation of their identity.

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[1]Accepted for publication March 10, 1959.

A Field Study of the Flight Behavior of the Tiger Swallowtail Butterfly[1]

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During the summer of 1957 a preliminary effort was made to mark Tiger Swallowtail butterflies (*Papilio glaucus glaucus* L.) and, after releasing them, to see if any of the marked specimens could be observed at the same location on subsequent days. On August 28 eight males were marked with rubber name and date stamps, using black ink. The yard in southern Maryland where the insects were marked was watched on the following days. One of the marked specimens returned on the second day, and two additional ones were recaptured on the fifth day after being marked. These results were very intriguing and led to a more thorough study in the summer of 1958 to gain information on the behavior of the Tiger Swallowtail butterfly.

The study area was the yard of the summer cottage owned by W. E. Lamb and situated on a ridge 500 yards inland on the western shore of the Chesapeake Bay at Breezy Point, Calvert County, Maryland. The area is separated from the water by a swamp and an open area with homes. To the north and west the yard is adjacent to dense woods mostly of oak, beech, and poplar. To the south the area is open for a short distance before joining a wooded area which is part of that extending around from the west. The immediate yard is open and planted with considerable shrubbery, trees, flower beds, and butterfly bushes which are the principal attractant for the butterflies, (fig. 1).

The butterflies were captured in a net. They were marked by holding the wings flat on the top of a killing jar and stamping the numbers as $\frac{5}{8}$-inch Roman numerals in red ink by using a figure 1 cut into the end of a No. 10 cork. The numbers were easily stamped on the insects by this method (fig. 1). The upper surface of the forewings was used. Both wings were utilized for the larger numbers. The writer has had considerable experience in tagging butterflies by this method, which was selected for use in this study rather than of that using gummed paper tags described by Urquhart (1955).

Seven males and a single female were marked on August 18, five males and two females on August 19, six males on August 20, seven males on August 21, nine males on August 22, and the last four males on August 24. Observations were made daily from the start of the marking through September 3 and then on Saturday and Sunday, September 6 and 7, and 13 and 14. A number of observers participated in this work. An almost constant vigil was kept by William E. Lamb, Jr., who spent a good part of every day checking the many Tiger Swallowtails that were attracted to the yard through September 3 and the two following weekends. This constant observation afforded a highly accurate count of the number of marked butterflies that returned to this yard.

The weather, which if adverse, could greatly affect an experiment such as this, was quite varied. During the week of marking the insects the days were clear and rain occurred on the nights of August 21 and 23. August 24 was very windy and it rained hard all day on August 25. August 26 was cloudy and the next day was clear. August 28 was cloudy, mild, and windy as Hurricane Daisy went up the Atlantic Coast. The remaining days were clear and it become cool after September 8. On August 30 the area was treated with insecticide from a mist blower employed for mosquito control.

The records of the captured or observed marked butterflies are tabulated in table 1. The date that the

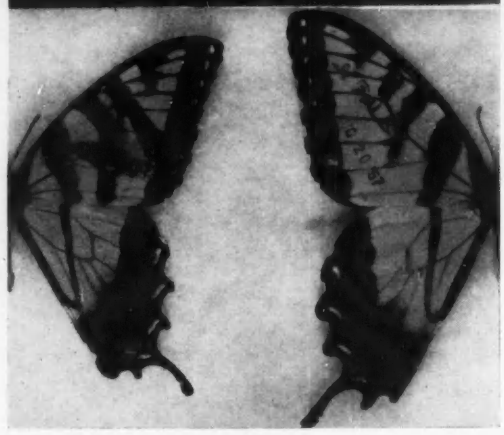

FIG. 1.—(Upper) Looking east from marking area showing distance from Chesapeake Bay.

FIG. 2.—(Center) Marking a butterfly.

FIG. 3.—(Lower) Marked butterflies.

[1]Accepted for publication March 20, 1959.

Table 1.—Returns of marked Tiger Swallowtail butterflies. All were male except number XII female. X equals date marked; R equals date of return.

Number of insect	Day of month—August 1958													
	18	19	20	21	22	23	24	25	26	27	28	29	30	31
I	X		R	R										
IV	X	R												
VI	X		R	R										
VIII	X	R	R											
XI		X												R
XII		X			R									
XIX			X				R			R		R	R	
XX			X	R										
XXII				X		R					R			
XXV				X		R			R					
XXIX					X		R							
XXXIV					X		R							
XXXVII					X								R	
XXXVIII							X		R			R		

individual specimens were marked is also given. All reoccurrences shown were in the yard in which they were marked except number IV, which was taken more than a mile away at Plum Point on the day after being marked. Another individual not included in the table was reported from the same area at a later date. Of the 41 butterflies marked, 13, or 32%, were definitely recaptured or observed in the yard where marked on one or more occasions up to 12 days later. In all, 34% or possibly 36% were recovered. Most of the returns were on the first to the third day after marking although six individuals occurred after the third day. This was a much greater return than had been anticipated, since the general area throughout the experiment (August 18 thru September 14) was highly populated with unmarked individuals of this same species.

The results show that certain individuals stayed in the area for several days at a time. Others left the area and reoccurred occasionally, while two individuals reoccurred only on the seventh and twelfth day after being marked. It is concluded that a good part of the male population of this species stays in a general area, although the size of this area was not determined. It was not determined how far some individuals wander. Of the three females marked, one returned to the area on the third day after being marked. Evans (1955), working with marked *Anthocaris reakirtii* Edwards, stated that "the females almost never return to the same area." The age of the marked insects was not known, but it is certain that some individuals of this species live in the field more than two weeks.

The writer acknowledges the assistance in this study of the following persons: David H. Fales, Mrs. John H. Fales, Mr. and Mrs. John C. Hancock, John C. Hancock, Jr., Bonnie L. Hancock, Randall W. Hancock, Richard Hayford, Mr. and Mrs. William E. Lamb, William E. Lamb, Jr., Margaret A. Mehler, Raymond McDermott, Geoffrey S. Parker, and Steven Seymour.

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